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Editor: Anton A. Reznicek

Editorial Committee: William R. Anderson, Howard Crum, Robert L. Shaffer

Part of the cost of publication of this volume was provided by funds from NSF grant DEB 79-04946 to Christiane Anderson, DEB 81-03522 to William R. Anderson and DEB 80-04178 to Rogers McVaugh.

Previous numbers of the *Contributions* are listed at the end of this issue. For information address the Director, University of Michigan Herbarium, North University Building, Ann Arbor, Michigan 48109, U.S.A. For issues previous to Volume 9, see inside back cover of Volume 14.

December 13, 1982

Contr. Univ. Mich. Herb. 15:1–92. 1982.

A MONOGRAPH OF THE GENUS *PEIXOTOA* (MALPIGHIACEAE)

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Ann Arbor, Michigan 48109

INTRODUCTION

Peixotoa is a genus of 28 species of yellow-flowered, wing-fruited vines and small shrubs whose center of diversity is the Planalto of Brazil. It is a very homogeneous assemblage that is characterized by large, cordate stipules, compound inflorescences composed of 4-flowered umbels, and a uniseriate androecium of alternating stamens and staminodes. Within the family this is a relatively recently evolved group in which the species have not greatly diverged. Attempts at studying *Peixotoa* were limited in the past by a paucity of good material and complicated by the occurrence of apomixis, which has not been suspected until now. The most recent monograph (Niedenzu, 1928) contained little information beyond that presented in Jussieu's study of 1843 and an unsatisfactory key. It is hoped that this treatment will provide a beginning toward a better understanding of this difficult genus.

TAXONOMIC HISTORY

St. Hilaire's collections from central Brazil included three species of Malpighiaceae which Adrien de Jussieu grouped into a new genus, *Peixotoa*, in his treatment of that family for St. Hilaire's *Flora Brasiliae Meridionalis* in 1832. The name commemorates Domingos Ribeiro dos Guimarãens Peixoto, a physician who had published "Dissertation sur les médicamens brésiliens" in Paris in 1830. Grisebach published three more species in 1839 based on Sellow collections. In 1840 Jussieu, who by then had seen collections of Claussen, Gaudichaud, Martius, and Salzmann, added seven more names when he published his "Malpighiacearum synopsis," which preceded the comprehensive monograph of the family of 1843. Turczaninow recognized a Blanchet collection as another new species in 1858. Kuntze described *P. cordobensis* from Argentina in 1898. However, his type is now included in *Cordobia argentea* (Griseb.) Niedenzu. Few collections and almost none from additional geographical areas had been made by the time Niedenzu published his monograph of *Peixotoa* in 1912. The limited material available to him was often scanty and in poor condition. In his treatment of the genus for *Das Pflanzenreich* (1928) he recognized 11 species and one variety in addition to numerous forms. With the exception of a new name published by Ferreira in 1969, little work has been done since Niedenzu. However, extensive field work within the last 30 years in the Planalto and adjacent regions has yielded a large number of collections of *Peixotoa*, including an astonishing number of novelties. In this treatment I recognize twenty-eight species, of which eighteen are new.

RELATIONSHIPS WITHIN THE FAMILY

Niedenzu (1928) divided the Malpighiaceae into two subfamilies, the *Planitorae*, characterized by a flat torus and wingless fruits, and the *Pyramidotorae*, characterized by a pyramidal torus and winged fruits. Morton (1968) substituted names based on included genera, since Niedenzu's names were not formed in accordance with the Code of Nomenclature. The *Pyramidotorae* thus became the *Gaudichaudioideae*. Niedenzu divided his *Pyramidotorae* into two tribes, the *Hiraeeae*, for genera in which the lateral wings are larger than the dorsal wing, and the *Banisterieae* in which the dorsal wing exceeds the lateral two. He placed *Peixotoa* into the latter next to *Banisteriopsis* (his "*Banisteria*"). Since Niedenzu based his scheme strictly on the torus and wing characters, it contains a number of unnatural assemblages. W. R. Anderson's current investigation of the infrafamilial structure of the *Malpighiaceae* will lead to changes in the present groupings (see Anderson, 1978). However, no matter how the family may eventually be subdivided, *Peixotoa* will be retained next to *Banisteriopsis*. This large and diverse genus is the most likely ancestor for the homogeneous, advanced *Peixotoa*.

With the exception of the "stipules," i.e. the two structures resulting from the fusion of the interpetiolar stipules, and the presence of the characteristic staminodes, all generic characters of *Peixotoa* occur in *Banisteriopsis* as circumscribed by Gates in her recent monograph (1982). While no single species shares all these characters, the following are found in the subgenus *Hemiramma* (*sensu* Gates): a vining habit; leaf glands borne on the lamina or petiole; 4-flowered umbels arranged in compound dichasia; sessile pedicels; calyx glands borne on the free part of the sepal and attached by their entire length; a corolla of yellow, glabrous petals with the posterior petal borne erect; glabrous anthers with the glandular connectives composed of large, inflated polygonal cells; a samara with a pair of lateral wings parallel to the areole; straight styles with capitate stigmas. In some species of *Banisteriopsis* the glandular connective becomes greatly enlarged while the size of the pollen sacs decreases, but completely sterile staminodes are not found. Yet, the pattern of reduction in the androecium is the same as in *Peixotoa* in that the change takes place in the stamens opposite the sepals. The composition of the androecium, i.e. fertile stamens opposite the petals alternating with sterile staminodes opposite the sepals, is constant throughout *Peixotoa* and was probably already established in the ancestor.

Three monotypic genera, *Cordobia*, *Mionandra*, and *Gallardoa*, from the southern edge of the family's range might be considered closely related to *Peixotoa*. In these three taxa the "stipules" also consist of the interpetiolar stipules which have fused into two cordate or triangular structures. In *Cordobia* and *Gallardoa* these may be bifid or entire with an acute or notched apex. Those of *Mionandra* are always bifid. In all three genera the inflorescence is reduced to a single flower with yellow, glabrous petals. Each androecium is similar to that of *Peixotoa* in that the stamens opposite the sepals are reduced to sterile structures. In *Cordobia* only tiny filaments are retained, while in *Gallardoa* and *Mionandra* the filaments, which are half as long or less than the stamen filaments, bear small apical glands. These glands are fusiform in *Gallardoa* and rhomboid in *Mionandra*. The pollen of *Cordobia* is like that of other Banisterioid genera, while that of *Mionandra* and *Gallardoa* is highly atypical (S. R. Lowrie, pers. comm.). One reason for grouping *Cordobia* with *Peixotoa* is its Banisterioid samara with its large dorsal wing and the usually present pair of lateral winglets. In the samara of *Gallardoa* the dorsal wing is reduced to a crest while the lateral wings are greatly enlarged. In *Mionandra* the change from a wind-dispersed samara to a detritus-fruit is reflected by the narrow, highly irregular crests that cover the mericarps. The vesture in all three genera is sericeous; the T-shaped hairs typical of *Peixotoa* are lacking. The erect, capitate styles of *Mionandra* are similar to those of some

species of *Peixotoa*. Those of *Cordobia* and *Gallardoa* are somewhat curved and bear most unusual, internal stigmas. In *Cordobia* the stigma is borne laterally along the broad edge of the apically flattened style. In *Gallardoa* the stigma is associated with an appendage, similar to the condition in *Stigmaphyllon*.

Though *Cordobia*, *Gallardoa*, and *Mionandra* have several characters in common with *Peixotoa*, I do not believe that these similarities form evidence that any or all of the three genera should be included in *Peixotoa* or are derived from it. The atypical inflorescences and the peculiar style of *Cordobia* and *Gallardoa* point toward a different origin. It seems more probable that they also arose from ancestors in *Banisteriopsis*.

ANATOMY AND MORPHOLOGY

Hair Types. The two basic hair types found in *Peixotoa* are Y-shaped and T-shaped. Pubescence composed of Y-shaped hairs is termed velutinous (Fig. 1a) and may occur on any part of the plant other than on the lower surface of the stem leaves. In the ovary and on the samara the stalks of these hairs are very short or the hairs may be subsessile. The T-shaped hairs have an unusually long stalk, which in most species is 0.2–0.5 mm long. In *P. gardneri* and *P. hirta* the stalks are 0.5–1 mm or more long. While standard in *Peixotoa* these hairs are only infrequently encountered in the rest of the family. When the stalk is sinuous or twisted and the trabecula is wavy or curled the resulting vesture is called tomentose (Fig. 1b). If the hairs are very densely intertwined and so numerous that the epidermis is obscured, the term woolly is used. However, no term exists that describes vesture composed of T-shaped hairs in which the trabecula and stalk are straight (Fig. 1c). Little purpose is served by coining yet another term. For the sake of clarity, surfaces covered with such hairs are here described as "pubescent with T-shaped hairs." *P. adenopoda* and *P. sericea* are the only species in the genus whose stem leaves have the true sericeous vesture that is a common condition in the rest of the family. These hairs consist of a long, straight, stiff, medifixed trabecula which is sessile or subsessile (Fig. 1d). In *Peixotoa* such hairs are also found on stipules and less frequently on inflorescence leaves.

Habit. While a small number of species are true vines with stems up to 8 m long, the majority are small shrubs ca 1–2.5 m tall. Yet, many of these shrubs form ascending or scandent branches that twine at the tips or may even switch to a vining habit if a suitable support is available. This flexibility suggests that the *Banisteriopsis* ancestor was probably a vine. *P. andersonii* is unusual in that it forms procumbent stems up to 4 m long that send up erect flowering axes. The stems of both vines and shrubs are terete and generally velutinous or sometimes tomentulose or both when young. The pubescence is generally abraded from the older parts. In *P. glabra*, *P. hatschbachii*, and *P. psilophylla* even the relatively young vegetative branches that bear inflorescences are glabrous at the time of flowering.

Stipules. The strikingly large stipules are a generic character in *Peixotoa*. Their presence or the characteristic stipule-scar permits even sterile material to be readily assigned to this genus. Each "stipule" is actually the product of fusion of the two opposing interpetiolar stipules. The two large, cordate structures that result from this fusion are decussate to the pair of leaves at that node. The stipules act as valvate bud scales. They may be glabrous or variously pubescent but are always finely and densely tomentulose along the margins. These marginal hairs interlock and act as a kind of seal when the stipules enclose the young shoot. The sides may be flat or recurved. Each stipule is commonly entire with an acute or, especially in the larger ones, notched apex or it may be bifid. While the stipules are necessarily concave when they act as bud scales, they usually become flat as the shoot matures. Yet in some species, especially in the inflorescence, the

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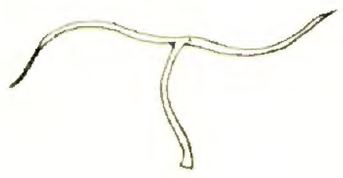

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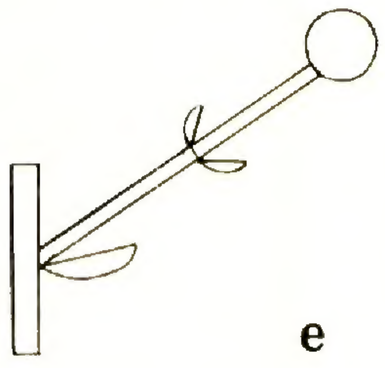

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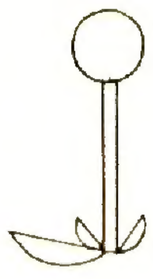

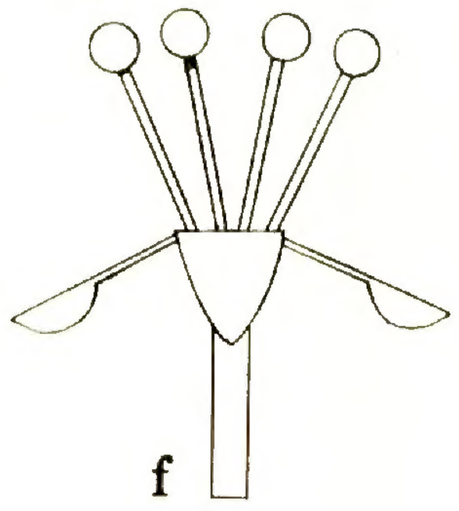

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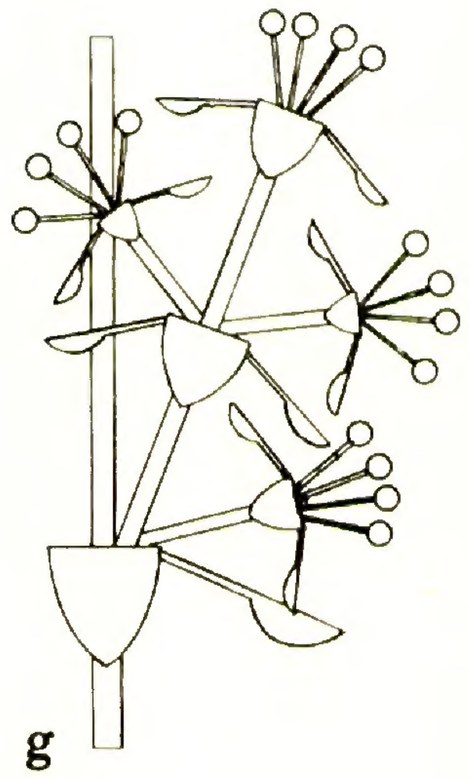

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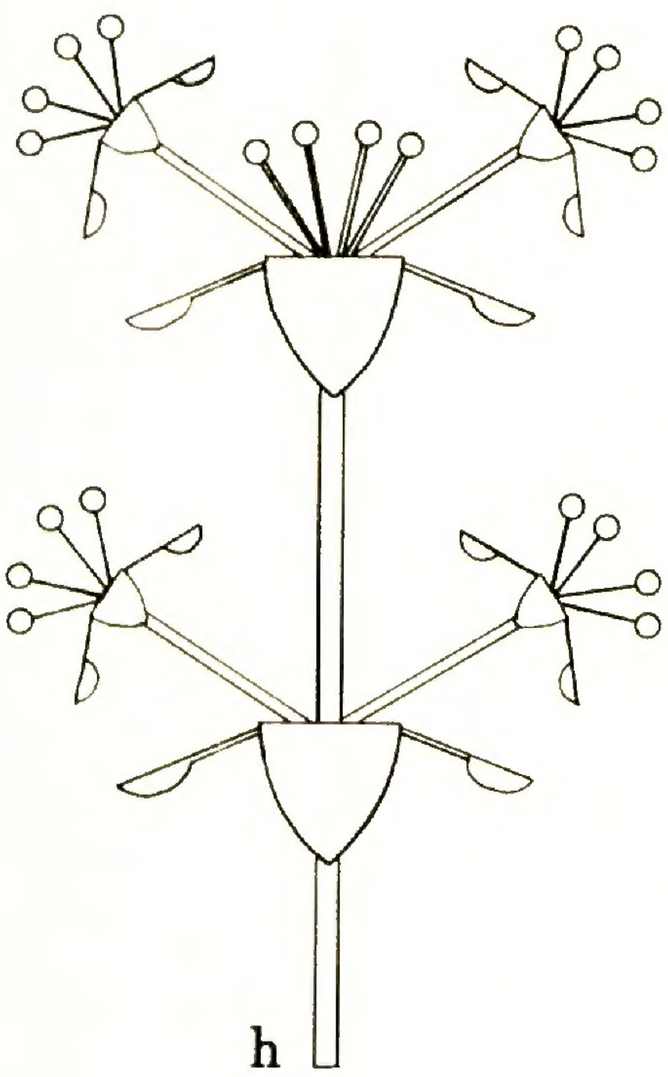

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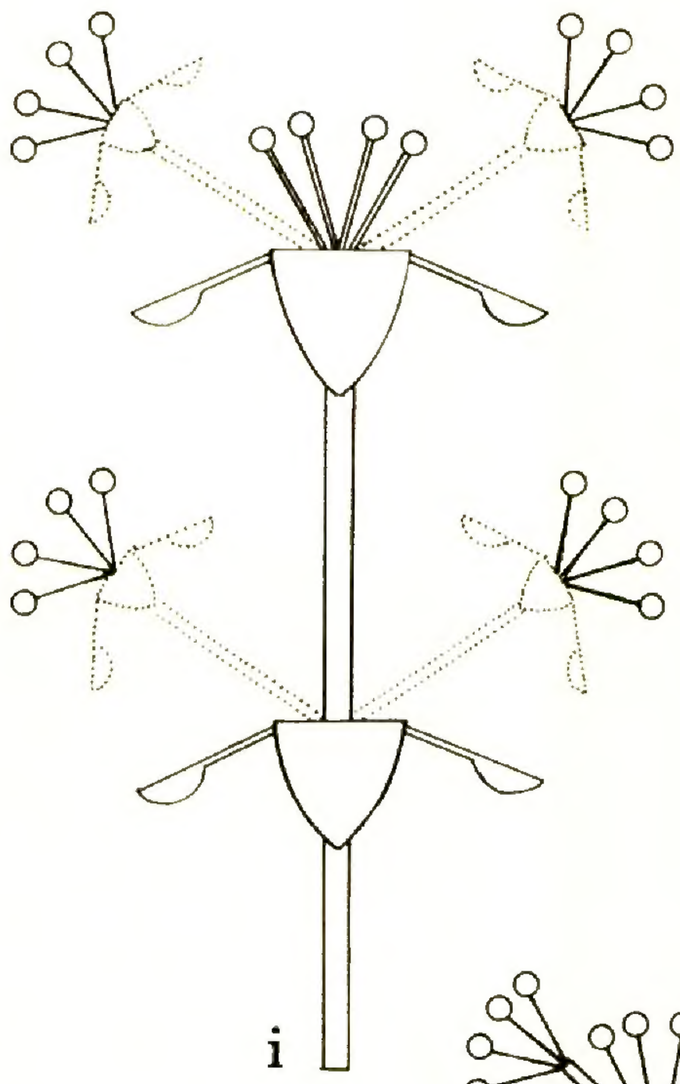

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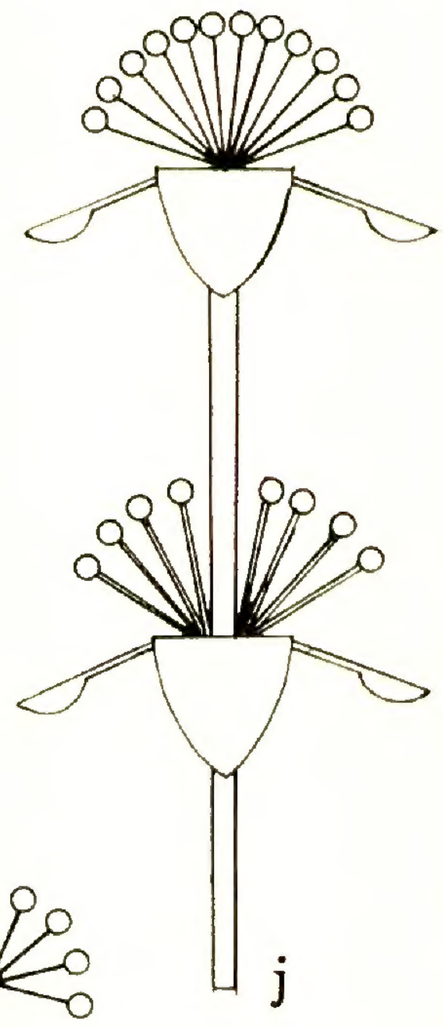

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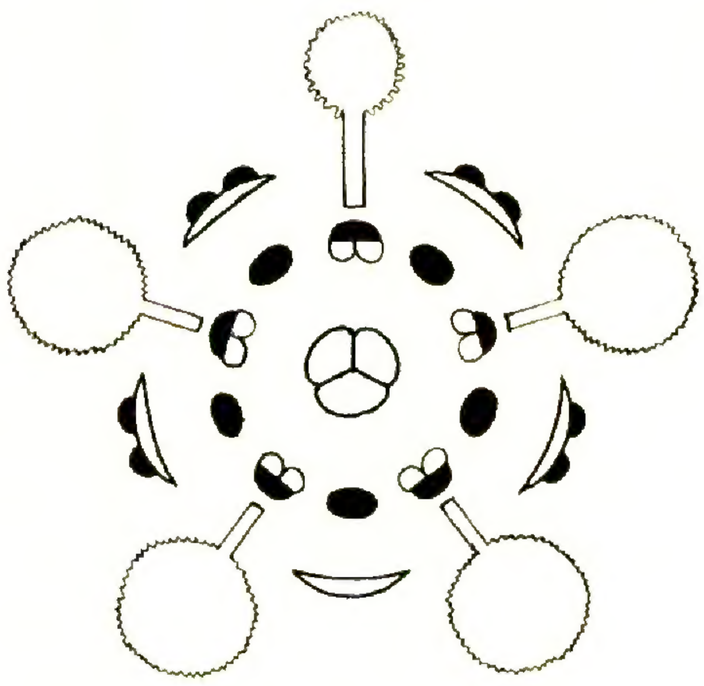

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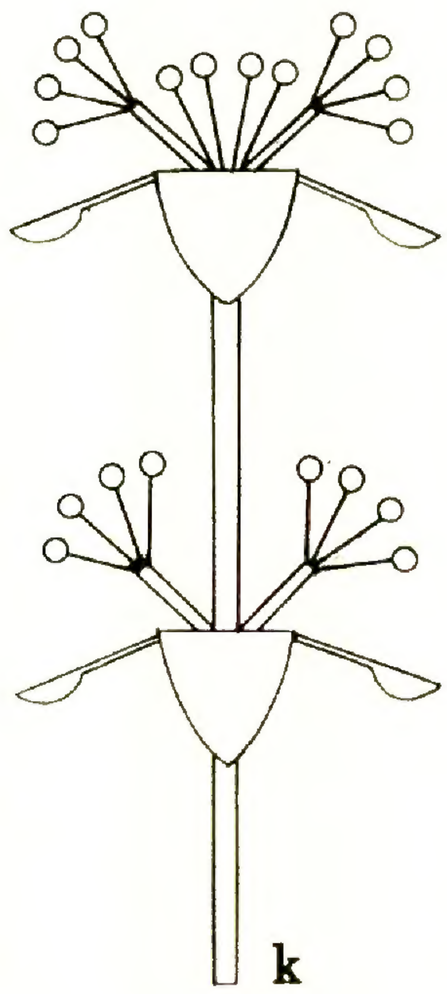

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FIG. 1. Hair Types and Diagrams of Inflorescence Structure and Flower (see section Anatomy and Morphology). Hairs representative of these vesture types: a) velutinous, b) tomentose, c) "pubescent with T-shaped hairs," d) sericeous. Inflorescence structure: e) hypothetical transition from pedunculate to sessile flower; f) typical umbel subtended by a pair of leaves and a pair of large stipules; g) "subsidiary axis" located between the secondary axis and the leaf; h–k) transition from 4-flowered (1-umbellate) terminal node to 12-flowered (3-umbellate) terminal node: h) all umbels 4-flowered, each umbel subtended by a pair of leaves and a pair of stipules, i–j) suppression of secondary axes accompanied by loss of leaves and stipules, terminal node 12-flowered, lateral nodes with a sessile umbel in each leaf axil, k) variation of condition in j: lateral umbels borne on secondary peduncles but not subtended by leaves and stipules. Floral Diagram: 1.

concave shape is retained. The stipules are usually largest on the stem and become decreasingly smaller toward the distal portion of the inflorescence. In a few cases the inflorescence stipules equal those of the stem or may exceed them. They are deciduous in most species but are persistent in some. In *P. cordistipula* they are retained in the inflorescence even after the leaves and pedicels are shed. In very large inflorescences the stipules of the most distal nodes may be lacerated or split into narrow strips of tissue, or sometimes the stipules are fused. In these cases it is common for the inflorescence leaves to be suppressed entirely.

Leaves. *Peixotoa*, like most Malpighiaceae, has opposite, decussate, simple, entire leaves. The petioles are terete and usually short, often less than 1 cm long. In some species, especially in vines, the petioles may be longer but never more than 3.5 cm long. The laminas are most commonly elliptical or ovate, but may also be obovate, rhombic, suborbicular, lanceolate or oblanceolate. While the apex is apiculate or sometimes acuminate, the tip is often broken off in the larger leaves, which then appear to be rounded or obtuse. The base is usually cordate or sometimes subtruncate. In *P. catarinensis* the larger leaves are cordate but the sinuses may be truncate. In the stem leaves of *P. sericea* the bases are cuneate. The margins are at least slightly recurved. Thick, almost coriaceous laminas are rugose. The veins are prominent below in all species. The vesture is variable. The laminas are sparsely to densely velutinous or glabrous above. Exceptions are *P. cipoana*, in which the laminas are sometimes tomentulose above, and *P. hirta*, in which they may bear T-shaped hairs and/or be velutinous above. Below, the laminas vary from glabrous to sparsely to densely pubescent with T-shaped hairs to sparsely to densely tomentose to woolly. *P. adenopoda* and *P. sericea* are the only species in which the stem leaves are sparsely sericeous above and more densely so below. The sericeous condition is common in the family but exceptional in *Peixotoa*.

As a rule the inflorescence leaves become gradually smaller toward the distal nodes, but sometimes the change is abrupt. The most proximal are usually similar to the most distal stem leaves. They usually change in shape toward the more distal nodes from lanceolate or triangular to linear and subulate. The presence or absence of a petiole in the more distal leaves is a good character for most species.

The leaf glands are always borne on the lower surface. Typically, each lamina bears two discoid or slightly oblong, prominent glands at the base, one on each side of the costa. Sometimes the glands are borne halfway on the petiole or rarely entirely on the petiole or rarely on the laminar tissue but very near the base and the costa. In the more distal inflorescence leaves the glands are usually disproportionately large and commonly cause the smallest leaves to become almost conduplicate. One to four additional smaller glands may be present. Most commonly they occur as a second pair adjacent to the larger glands. These additional glands are found especially in the inflorescence leaves. At times they become variously fused, especially so in the inflorescence leaves, where, in the most extreme cases, a band of glandular tissue extends across the base of the lamina. In *P. leptoclada* and *P. paludosa* the more distal inflorescence leaves may have a glandular tip. In *P. adenopoda*, *P. catarinensis*, *P. paludosa*, and *P. spinensis* the leaf glands are borne on the proximal ⅓ of the surface of the lamina, usually approximately equidistant from the base and costa. In *P. sericea* the glands are borne above the base and at or very close to the costa but at different levels, rather than equidistant, from the base. In *P. jussieuana* the glands may be at the base or on the laminar surface. The larger leaves of *P. leptoclada* may have one pair at the base and a second pair on the lamina, or on the same plant some of the largest leaves may bear a pair of glands on the lamina only and lack the basal pair. In the more distal inflorescence leaves the glands are always basal regardless of the position of the glands on the stem leaves. Though prominent, the

glands of most species are sessile. In the stem leaves of *P. adenopoda* and *P. hatschbachii* they are stalked. This stalk is ca 0.8–1.2 mm long. Glands of the more distal inflorescence leaves of these species are sessile. In some species one or both glands are sometimes lacking.

Inflorescence. The basic unit of the inflorescence is a 4-flowered umbel. This is so thoroughly established in the genus that it was probably already present in the *Banisteriopsis* ancestor. Each umbel is an extremely reduced 4-flowered raceme [the pseudoraceme of Cuatrecasas (1958) and Anderson (1981)] in which the axis is foreshortened and in which the primary peduncle is lost (Fig. 1e). This legacy is reflected in the maturation pattern of the four flowers: two are always at least slightly older than the other two. Typically each umbel is sessile or subsessile at the node and subtended by a pair of leaves and by the pair of stipules which functioned as bud scales (Fig. 1f). The sessile pedicel of each flower is subtended by a much reduced, non-vascularized bract and a pair of equally reduced bracteoles. These scale-like structures vary from triangular to oblong to semicircular to subrectangular and are glabrous or variously pubescent. They are persistent though in some species occasionally absent. The pedicel is extremely variable in size in all species. It may increase up to ½ of its length in fruit and always becomes a little stouter. It is always pubescent even in species which are otherwise glabrous.

The umbels are arranged into compound dichasia and thyrses, which are terminal and/or axillary. Solitary umbels are common only in *P. axillaris* and *P. hispidula*. In large inflorescences, especially in vines, additional axes are sometimes produced between the inflorescence branch and the leaf (Fig. 1g). Such subsidiary axes are always much smaller than the axes with which they are associated.

In *P. adenopoda, P. catarinensis, P. parviflora, P. tomentosa* and a few individuals of *P. reticulata*, the secondary inflorescence axes with their stipules and leaves are suppressed at the more distal nodes. As a result of this change the umbel borne on such a secondary axis now becomes sessile in the axil at the branch point. At the terminal node the central umbel is flanked by two sessile umbels, which results in a three-umbellate condition (Fig. 1h–j). The terminal nodes of these species are thus always 12-flowered. Commonly, when such a reduction of the inflorescence branches has taken place, the umbel instead of being sessile is supported by a secondary peduncle (Fig. 1k). This secondary peduncle differs from a typical inflorescence axis in that it lacks the stipules and leaves. Its length is variable within an individual inflorescence. Sometimes the bracts occur down on the secondary peduncle.

Peixotoa octoflora is unique in the genus in that each umbel is composed of four pairs of flowers. In each pair one pedicel is sessile while the second pedicel is borne on a short (1–2.5 mm long) primary peduncle (Fig. 21b). The umbels are grouped into a compound inflorescence typical for *Peixotoa*. A primary peduncle is otherwise only very rarely encountered in some individuals of *P. reticulata*.

Flower. The terminology used here to describe the various floral parts follows that of Niedenzu (1928), Cuatrecasas (1958), and Anderson (1981), and is illustrated in Fig. 1l. The flowers of *Peixotoa* are bilaterally symmetrical with the odd, fifth petal in the posterior position. The remaining petals are grouped into an anterior-lateral pair and a posterior-lateral pair. These petals are reflexed between the sepals, while the posterior petal is erect. The eglandular sepal is designated the anterior sepal, while the other four, like the lateral petals, are grouped into an anterior-lateral pair and a posterior-lateral pair. The plane of symmetry passes through the posterior petal and the anterior sepal. The position of the stamens and staminodes is indicated by the perianth part they oppose. Thus, the stamen opposite the posterior petal is called the posterior stamen. The

3-carpellate ovary is placed so that the plane of symmetry passes through the anterior carpel and between the two posterior carpels. The designation of the style follows that of its carpel, i.e. the anterior style belongs to the anterior carpel. The posterior carpels and styles are alike. No distinction is made between them.

Within the genus the size and to a lesser extent the shape of the floral parts vary, but the arrangement is constant and permits visits by oil-collecting bees in the manner described by Vogel (1974) and Anderson (1979). In brief, the bee lands on the center of the flower, orients itself by the posterior petal, the "flag," whose claw it grasps with its mandibles, and with its front and middle legs reaches between the lateral petals to scrape oil from the calyx glands. Some bees also collect pollen. The oil and pollen are transferred to the hairy hind legs and carried to the nest to serve as food for the larvae. During the bee's visit pollen is rubbed on the underside of the bee and presumably transferred to the stigmas of the next flower visited. The claw of the flag petal of a visited flower commonly shows two lateral indentations which are caused by the pinching grasp of the bee's mandibles.

Sepals. The five valvate sepals are ovate or broadly oblong with an acute apex which becomes recurved or revolute when the flower opens. They are glabrous or variously pubescent adaxially and densely velutinous abaxially. All are densely tomentulose along the margins. These hairs interlock when the sepals are closed in bud. All except the anterior sepal bear a pair of oblong glands on the proximal 1/3–1/2 of the free part of the sepal. These glands are green in nature and turn dark brown upon drying. The anterior sepal is usually a little narrower than the lateral four.

Petals. The five petals are yellow, glabrous, and clawed. The four lateral petals are of equal shape and usually of equal size, though the anterior-lateral two are sometimes a little larger than the posterior-lateral two. The flat limb varies from elliptical to obovate to orbicular. *P. andersonii* is unique in that the limbs of its lateral petals are oblanceolate. The margin is usually fimbriate, sometimes denticulate, or sometimes both. The fimbriae and teeth commonly bear tiny glands. The posterior petal, the "flag," differs markedly from the other four. The claw is much longer than and about twice as thick as that of the lateral petals and is continuous with the limb. The posterior limb is also flat, but usually notably smaller than and often of a different shape than the lateral limbs. The margin is either entirely capitate-glandular or only so in the proximal 1/3–4/5 with the distal part fimbriate- or denticulate-glandular.

Androecium. The uniseriate androecium is composed of five fertile stamens, opposite the petals, alternating with five sterile staminodes, opposite the sepals. The filaments are connate at the base. The four lateral stamen filaments are usually equally long, but sometimes the anterior-lateral two exceed the posterior-lateral two a little. They are straight or, if very long, curved in the distal ¼ toward the ovary. The posterior stamen filament is usually much shorter than the lateral four and is commonly arced toward the posterior petal. The anthers are basifixed and glabrous. They are all of equal size and have longitudinal, introrse pollen sacs. A prominent glandular connective projects ca 0.3–0.5 mm above the locules; it is lacking only in *P. anadenanthera*. The pollen is apparently released at or just prior to the opening of the flower. In apomictic plants the pollen sacs usually remain closed.

Stuart R. Lowrie, who is completing a comprehensive study of pollen in the Malpighiaceae, has kindly provided me with his findings in *Peixotoa*. The pollen grains of *Peixotoa* are of the cuboidal type that Lowrie believes is unique to the family and typical of most of the genera in Niedenzu's tribe *Banisteriae*. In *Peixotoa* each grain has 12 rugae and 6 pores (Fig. 2). The pores are not placed at the corners of the cube but slightly removed from them. Lowrie determined that they are located at the points of coincidence of an octahedron inscribed in the

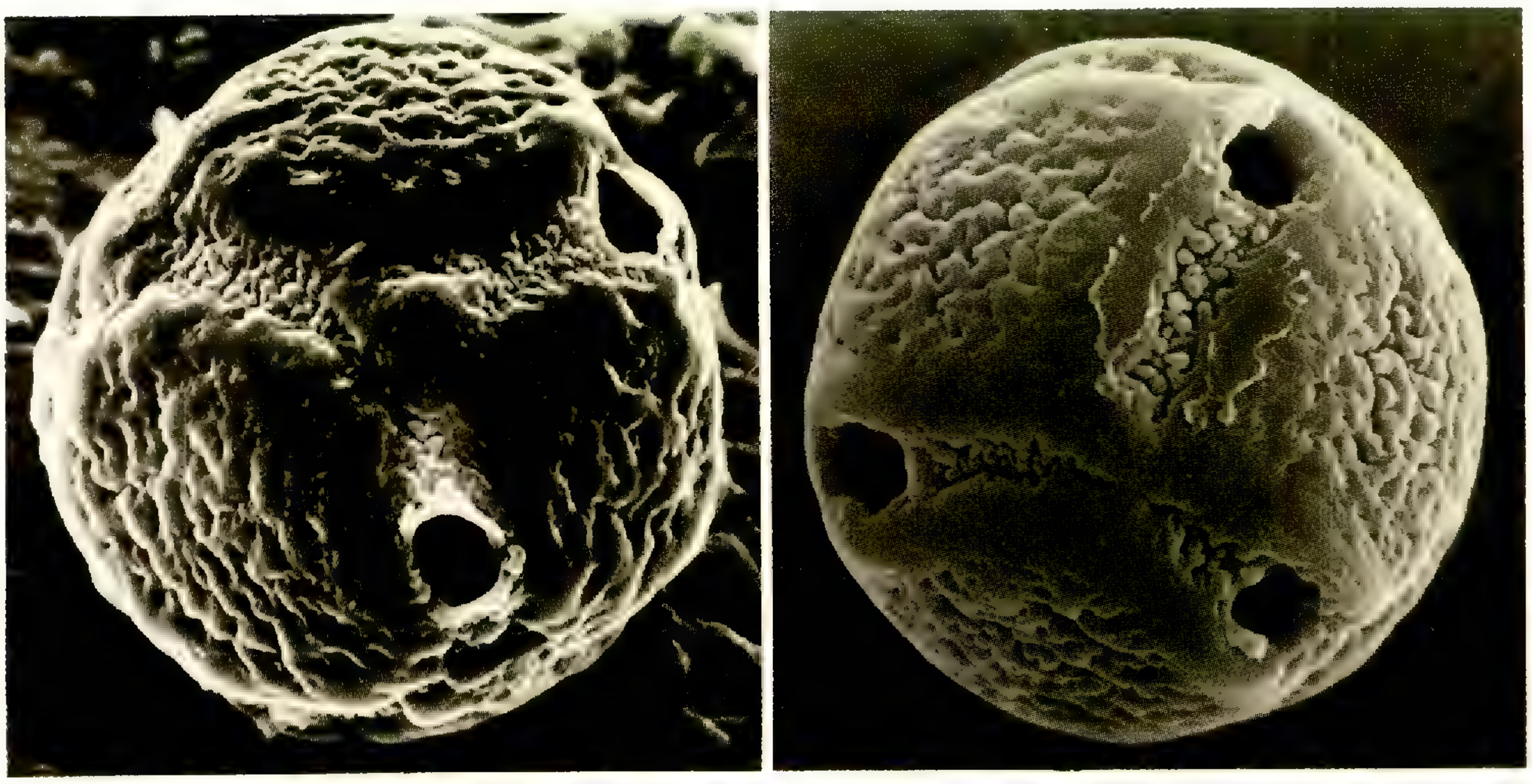

FIG. 2. Pollen of *Peixotoa*. Left, *P. goiana*, × 1300 (*Irwin et al. 17562*); right, *P. parviflora*, × 1300 (*Dusén 9225*). SEM photographs by S. R. Lowrie.

cube. Though there is considerable variation in the sculpturing of the pollen grains among the species of other genera, the pollen of the various species of *Peixotoa* is relatively uniform. The sizes given in the species descriptions, based on measurements of pollen grains placed in water, range from 42 to 74 μm.

The slender staminode filaments are about half as thick as the stamen filaments and taper toward the apex. Each filament bears a basifixed, obovoid or sometimes spherical gland at the apex. The adaxial face of the gland has a groove in the proximal 1/3–3/4 (–7/8). The apex and abaxial surface are either smooth or the apex has a shallow to deep indentation which is decurrent on the abaxial face. If the indentation is very deep, the glands appear cordate. In *P. irwinii* the apex is smooth, but the abaxial face has a shallow and broad depression. Individual glands bearing one or even two small locules occur in *P. magnifica*, but are rare. Such locules are 0.7–1 mm long, contain largely aborted pollen, and remain closed. The anterior staminode is usually the largest but may equal the anterior-lateral two. The posterior-lateral two are usually the smallest. While the anterior and anterior-lateral filaments are erect, the posterior-lateral two are commonly inflexed between the posterior styles.

Gynoecium. The 3-carpellate, 3-loculate ovary is densely velutinous. Each locule is fertile and contains one anatropous, pendent ovule. The styles are free to the base and persistent in fruit. The anterior style is longer or shorter than or equal to the posterior two but always a little stouter. It may be erect but more commonly is arced or inclined toward the posterior petal, rarely toward the anterior sepal. The posterior styles are usually divergent and variously inclined toward the posterior-lateral petals. In *P. parviflora* they are curved toward the anterior-lateral petals. All styles are glabrous or may be very sparsely velutinous, especially near the base. The stigmas are terminal and in nearly all species capitate. The exceptions are *P. jussieuana* and *P. magnifica*, in which the anterior stigma is oblong and borne on the abaxial surface at the apex of a long, strongly curved style.

Fruits. The fruits of *Peixotoa* are schizocarps in which each mericarp develops into a velutinous samara. The samaras are grouped around a pyramidal torus and at maturity are suspended by a carpophore. Each samara bears a large dorsal wing which is thickened along the curved, sigmoid, or arced, entire upper (adaxial) margin. The lower margin may be straight, sigmoid or semicircular

and, though at times entire, is commonly somewhat erose. The dorsal wing is usually broadest at the middle or beyond. Each nut also bears two lateral winglets, which are much smaller than the dorsal wing. These are usually rectangular, and entire, erose or coarsely dentate. In some species the lateral wings are semicircular and recurved and give the samara an inflated appearance. In *P. hatschbachii* the lateral wings are absent or reduced to a narrow strip of tissue less than 1.5 mm wide or to a crest. The dorsal and lateral wings are confluent at the base of the nut and sometimes extend into a tooth. The ovoid nut has a triangular or cordate, concave areole. At maturity the seed fills the locule. The embryo has obspatulate, unequal cotyledons. The outer cotyledon is always larger and folded over the inner one. The inner cotyledon may also be folded or may be straight. Sometimes the apices are twisted.

CHROMOSOME NUMBERS

Counts of n=10 have been obtained for *P. glabra (Anderson 11549)* (W. R. Anderson, pers. comm.) and *P. hispidula* (Ormond *et al.*, 1981). Since n=10 is the base number for *Banisteriopsis* (Gates, 1982), the most probable ancestor of *Peixotoa*, it is most likely that this is also the base number for *Peixotoa*. Counts have also been made of pollen mother cells of the apomictic *P. reticulata* (*Anderson 11790*). Here 2n=30, but the separation at anaphase I/telophase I is highly irregular. Figures of 17 and 13, 16 and 14 as well as of 15 and 15 pairs occur (W. R. Anderson, pers. comm.). The pollen grains of the voucher, as in the great majority of the specimens of *P. reticulata*, are largely aborted. *P. reticulata* may be a triploid that resulted from a cross between a diploid and a tetraploid. N=15 is otherwise unknown in the Malpighiaceae.

DISTRIBUTION

Peixotoa is composed largely of small shrubs from the cerrados of the Brazilian Planalto and adjacent areas. Vines are commonly found also in woodlands, gallery forests and at forest margins. Three species from Bahia, *P. adenopoda*, *P. paludosa*, and *P. sericea*, and also *P. jussieuana* are reported from caatingas. *P. catarinensis* and *P. hispidula* are coastal species that grow in the coastal forests, restingas, on dunes, and on beaches.

Like many other Planalto groups, *Peixotoa* is characterized by a high degree of endemism. Twenty of the twenty-eight species are found in Minas Gerais and Goiás, of which only two are common to both states. Of the twelve occurring in Minas Gerais, eight are known only from that state. Of these, seven have been reported only from the Serra do Espinhaço. Five of the eight species occurring in Goiás are endemics. Four species are known only from Bahia. Only one species, a coastal endemic, is found in Santa Catarina. Only five species have relatively wide ranges. *P. hispidula*, the other coastal species, ranges from Bahia to Rio de Janeiro. It has also been collected twice from São Paulo. *P. parviflora* occurs in central and southern Minas Gerais, Rio de Janeiro, São Paulo and Paraná. *P. magnifica* is a vine of central and southern Goiás, central Mato Grosso and eastern Bolivia. The range of *P. jussieuana*, a close relative, extends from Ceará to Piauí and Maranhão. It has been collected once in Paraná (an atypical plant). The most widespread species is the apomictic *P. reticulata*. It is common from southern Minas Gerais, southern Goiás and southern Mato Grosso to São Paulo, Paraná, eastern Paraguay, and eastern Bolivia.

APOMIXIS

Apomixis has not been previously reported in *Peixotoa*. The findings noted here are only a preliminary report. In this treatment "suspected apomicts" will

simply be called "apomicts" for the sake of brevity but also with the understanding that only a thorough study to be undertaken in the future will reveal the mechanisms involved.

Apomixis apparently occurs in five species. In *P. leptoclada* the apomicts are more robust than the sexual individuals but otherwise resemble them closely. There is no such gross morphological difference between the sexual specimens and the one known apomictic collection (*Roth 1587*) of *P. paludosa*. *P. axillaris* and *P. octoflora*, while clearly distinct taxa, are known only from apomictic material. Since both are from little-collected areas, sexual populations may well be discovered during future field work. The commonest *Peixotoa* is *P. reticulata*, which doubtlessly owes its wide distribution to apomixis.

In the flowers of apomicts the anthers never open and contain largely aborted pollen grains that are 88–99% non-staining in cotton blue in lactophenol. The few grains that do stain are often large and are perhaps unreduced pollen mother cells. Exceptions have been noted only in some individuals of *P. reticulata*. In *Krapovickas & Cristóbal 34372* almost 100% of the pollen, contained in closed anthers, does stain; yet, the grains are abnormal in that they are small and very thick-walled. In a few specimens some flowers do have open anthers which often contain a lower percentage of non-staining grains than do closed anthers. For example, in *Fiebrig 4590* pollen from the open anthers is 45% non-staining, while pollen from closed anthers is 94% non-staining. However, in *Hatschbach 21770* the pollen from closed as well as from the few open anthers is only ca 3% non-staining. Only two collections are known in which all flowers have all anthers open. In *Mexia 5798*, the staining of the pollen is highly variable. The percentage of grains that do not stain ranges from 45–89% per anther. In the second collection, *Occhioni 5775*, nearly all the grains do stain. Perhaps this is a rare sexual individual. Examination of pollen mother cells of *P. reticulata* (*Anderson 11890*) revealed that while 2n=30, the separation at anaphase I/telophase I is highly irregular with 17 and 13, 16 and 14, or 15 and 15 pairs segregating to the opposite poles (W. R. Anderson, pers. comm.). Such irregular meiosis would account for the high percentage of aborted pollen. Yet, if occasionally the separation is regular, some functional pollen could be produced. Since the anthers do open sometimes in some individuals, it may be possible for an apomict to function as a male parent. Of course, it is also possible that an apomict may function as a female parent.

In areas where the range of *P. reticulata* overlaps with that of sexual species, some hybridization apparently does take place. *Anderson 8564* from the Gouvêia-Diamantina area in Minas Gerais has the glabrous foliage and the indented staminode glands of *P. glabra* but otherwise is like specimens of *P. reticulata* in that area. A number of collections from southern Goiás and the Distrito Federal are intermediate in various flower characters between *P. reticulata* and *P. goiana*. *Hatschbach 2465* from Terenos, Mato Grosso, has fruits similar to those of *P. magnifica* in that the dorsal and the lateral wings are relatively large and extend into a long (ca 0.5 cm) tooth below the nut. Other collections from southern Mato Grosso and also from Paraguay have some attributes of *P. cordistipula*, a species of central Mato Grosso and eastern Bolivia. The readily recognizable regional types have perhaps originated as sterile hybrids that were apomictically propagated.

The apomicts are morphologically highly variable, especially in the shape and size of the flower. On the other hand, the differences in curvature and size, especially in length, of the stamens, staminodes and the styles are minimal. In sexual species these differences are generally constant. In apomictic individuals, especially of *P. reticulata*, it is not unusual to encounter flowers in which the stamens, staminodes and styles are subequal and erect. Teratologies, such as flowers with extra floral parts, have been noted in apomicts but are exceedingly

rare in sexual species. All of these morphological changes in the apomictic plants may reflect the relative unimportance of presenting the flower to the pollinator to assure seed set.

The fruit set in apomictic plants tends to be unusually high, often 100% or nearly so. Apparently maturation of the fruit begins soon after the flowers open. In *Irwin 17830* it seems to begin even earlier. Here the petals do not expand but are lifted like a cap and then shed by the developing fruit. Study of the seeds shows that polyembryony is sometimes involved. Often the seed contains both a normal embryo and an additional, smaller one. This extra embryo is commonly misshapen or may be an unformed mass of tissue.

TAXONOMY

Peixotoa Adr. Jussieu in St. Hilaire, Fl. Bras. Mer. **3**: 60. 1832 [1833].

Vines or shrubs or subshrubs with erect, ascending, scandent, pendent, or procumbent branches. Vegetative branches glabrous or velutinous or tomentose when young, the pubescence commonly abraded from older parts. Stipules large, interpetiolarly connate, the pair cordate or triangular, entire with the apex acute or notched or bifid, variously pubescent or glabrous adaxially and abaxially, persistent or deciduous, margins tomentulose, flat or recurved; inflorescence stipules often concave, enclosing immature umbels. Leaves opposite and decussate, petiolate, the lamina simple, often rugose, ovate, elliptical, obovate, rhombic, suborbicular, lanceolate, or oblanceolate, the apex apiculate or sometimes acuminate, the base cordate or subtruncate, velutinous or glabrous above (sericeous in *P. adenopoda* and *P. sericea*, sometimes tomentulose in *P. cipoana*), pubescent with T-shaped hairs, tomentose, woolly or glabrous below (sericeous in *P. adenopoda* and *P. sericea*), the veins prominent below, margins entire, recurved, with a pair of glands at the base at the costa or borne in the proximal ⅓ of the lamina away from the base and costa, sometimes with 1 to 4 smaller, additional glands, these sometimes variously fused, or the glands absent; glands discoid or slightly oblong, prominent, sessile (stalked in *P. adenopoda* and *P. hatschbachii*). Inflorescence leaves smaller than the cauline, petiolate or sessile, lanceolate, oblanceolate, triangular, linear, or subulate. Inflorescence terminal and/or axillary, of 4-flowered umbels (8-flowered in *P. octoflora*), borne in compound dichasia or thyrses with axes to the 6th order (or the umbel solitary in *P. axillaris* and *P. hispidula*), with 1 sessile umbel per node, or the distal lateral branches suppressed and then the terminal nodes with 3 umbels and the subterminal nodes with 1 or 2 umbels per leaf axil, these umbels sessile or borne on secondary peduncles, primary peduncles absent (present in *P. octoflora*). Bracts and bracteoles present and persistent, or absent, triangular, oblong, semicircular, or subrectangular, variously pubescent or glabrous. Pedicels pubescent, always stouter and commonly longer in fruit. Sepals 5, valvate, ovate or broadly oblong, apex acute, recurved or revolute, variously pubescent or glabrous adaxially, densely velutinous abaxially, margins tomentulose, the anterior sepal eglandular, the 4 lateral sepals each with a pair of oblong glands entirely borne on the free part of the sepal in the proximal ⅓ or ½. Petals yellow, glabrous, clawed, the limb orbicular, obovate, or elliptical (oblanceolate in *P. andersonii*), the 4 lateral petals equal or subequal, the margins fimbriate or denticulate or both, glandular or eglandular, the posterior petal with a thicker, longer claw and a usually smaller limb than the lateral petals, its margin capitate-glandular or only so in the proximal part, the distal section fimbriate- or denticulate-glandular. Androecium uniseriate, the filaments connate at the base; fertile stamens 5, opposite the petals, the 4 lateral filaments equal or subequal, erect, the posterior filament usually shorter, arced or inclined toward the posterior

petal or erect, anthers basifixed, glabrous, with a prominent glandular connective (absent in *P. anadenanthera*), pollen sacs longitudinal, introrse, pollen cuboidal, with 12 rugae and 6 pores. Staminodes 5, sterile, opposite the sepals, the filaments ca ½ as wide as the stamen filaments, tapered, the anterior and anterior-lateral filaments erect, the posterior-lateral filaments usually inflexed between the posterior styles, bearing apical glands (modified sterile connectives), the glands basifixed, obovoid or spherical, glabrous, with a groove in the proximal 1/3–3/4 (–7/8) in the adaxial face, the apex smooth or with a shallow or deep indentation decurrent on the abaxial face (in *P. irwinii* the apex smooth, the abaxial face with a broad, shallow depression), the anterior and anterior-lateral staminodes usuallly larger than the posterior-lateral 2. Ovary densely velutinous, three-carpellate, three-loculate, with one anatropous, pendent ovule. Styles 3, free to the base, glabrous or sparsely velutinous, especially near the base, the anterior style arced or inclined toward the posterior petal or erect, longer or shorter than or equal to the posterior two, the posterior styles usually divergent, curved or inclined toward the posterior-lateral petals (toward the anterior-lateral petals in *P. parviflora*), stigmas terminal, capitate (in *P. magnifica* and *P. jussieuana* the anterior stigma oblong and borne at the apex but laterally on the abaxial surface). Torus pyramidal. Fruit schizocarpic, each mericarp a samara, velutinous, suspended by a carpophore, with a large dorsal wing and 2 much smaller lateral winglets (these much reduced or absent in *P. hatschbachii*), the 3 wings sometimes forming a basal tooth, areole cordate or triangular, nut ovoid, the mature seed filling the locule, the embryo with unequal, obspatulate cotyledons, the large outer cotyledon folded over the smaller, folded or straight, inner cotyledon. Chromosome number n=10.

Lectotype. *Peixotoa glabra* Adr. Jussieu.

NOTES ABOUT THE KEY TO THE SPECIES

Peixotoa is a homogeneous genus whose species are often separated on the basis of microscopic characters. To use this key it is essential to have an understanding of the structure of the flower and of the inflorescence. The reader who is not familiar with the genus is urged to read the section Anatomy and Morphology and to consult Fig. 1. The terminology used follows that of Niedenzu (1928), Cuatrecasas (1958), and Anderson (1981). It is necessary to revive dried flowers to ascertain the shapes and sizes of the petals, stamens, staminodes, and styles. For this purpose Pohl's solution (Pohl, 1965) was found to be a superior wetting agent. Measurements for floral parts, except for the sepals, are taken from revived material. The measurements for the wings of the samara are indicated as follows. In the dorsal wing the distance from the attachment at the nut to the farthest margin is the "length"; the maximum measurement at right angles to this length is the "width." For each lateral winglet, the maximum measurement from the attachment at the nut to the farthest margin is the "width"; the maximum measurement at right angles to this width is the "height." Since a large number of species are endemics, geographical ranges are listed in the key. The discussion following each species description cites the most distinguishing characters which help to separate that species from morphologically similar species and from those within its range. The reader may also find it useful to refer to the illustrations which are provided for each species.

P. reticulata is an apparently apomictic and polyphyletic assemblage. The anthers of all or of nearly all flowers remain closed. This condition is used here to key *P. reticulata*. Of all the collections examined only two have all anthers open. This condition has been omitted from the key. Since *P. reticulata* is highly variable and apparently hybridizes with some sexual species, structuring the key

to include all the possible morphological variation for this exceedingly rare condition would make the key extremely complicated and difficult to use. Therefore, the reader is cautioned that if his specimen, bearing open anthers, does not key and is from the range of *P. reticulata*, he may have another such rare individual. In such a case, it is suggested that for correct determination the description and illustrations of *P. reticulata* and of the sexual species of the same range be compared.

KEY TO THE SPECIES OF *PEIXOTOA*

1. Lower surface of the stem leaves glabrous or very sparsely pubescent with the few hairs restricted to the major veins and margins.
   2. Anthers closed. (Minas Gerais) 25. *P. reticulata.*
   2. Anthers open.
      3. Glands of the stem leaves stalked. (Goiás) 13. *P. hatschbachii.*
      3. Glands of the stem leaves sessile or absent.
         4. Inflorescence commonly of 1 or 3 or 5 umbels, occasionally more, 3° axes absent; all inflorescence leaves petiolate; limb of the lateral petals 13–20 mm long; anterior and anterior-lateral staminode glands wider than long. (Coastal regions from Bahia to São Paulo) 15. *P. hispidula.*
         4. Inflorescence of more than 5 umbels, 3° axes usually present; the more distal inflorescence leaves sessile or subsessile; limb of the lateral petals 7–14 (–16) mm long; anterior and anterior-lateral staminode glands longer than wide or as long as wide.
            5. Limb of the posterior petal (4–) 5.2–7.5 mm long, (3.2–) 3.8–4.5 mm wide, oblong, elliptical, or obovate; limbs of the lateral petals with a fimbriate margin.
               6. Petioles glabrous; limbs of the lateral petals orbicular; staminode glands of equal size; anterior style shorter than the posterior two. (Minas Gerais) 11. *P. glabra.*
               6. Petioles golden velutinous; limbs of the lateral petals obovate; anterior and anterior-lateral staminode glands larger than the posterior-lateral two; anterior style equal to the posterior two. (Minas Gerais) 16. *P. irwinii.*
            5. Limb of the posterior petal 7.5–9 mm long, 6.8–10 mm wide, orbicular or obovate; limbs of the lateral petals with a fimbriate and/or denticulate margin.
               7. Pedicels and inflorescence leaves densely white velutinous; limb of the posterior petal 8.5–9 mm long, 8.5–10 mm wide, obovate; limbs of the lateral petals 11–14.5 mm wide, the margin denticulate; filaments of the posterior-lateral staminodes 3.4–3.8 mm long, the glands 1.2–1.3 mm long, 1.1–1.2 mm wide; anterior style inclined toward the posterior petal. (Mato Grosso) 24. *P. psilophylla.*
               7. Pedicels and inflorescence leaves usually golden (sometimes white) velutinous; limb of the posterior petal 7.5–8.3 mm long, 6.8–8 mm wide, orbicular; limbs of the lateral petals 9–12 mm wide, the margin fimbriate and/or denticulate; filaments of the posterior-lateral staminodes 2.8–3.5 mm long, the glands 1–1.1 mm long, 0.9–1 mm wide; anterior style erect. (Goiás) 12. *P. goiana.*
1. Lower surface of the stem leaves pubescent, hairs not restricted to the major veins and margins.
   8. Terminal inflorescence nodes bearing more than 4 flowers.
      9. Glands of the stem leaves borne on the surface of the lamina away from the base and costa, or absent.
         10. Glands of the stem leaves stalked, 0.8–1.5 mm in diameter; anterior and anterior-lateral staminode glands with an indentation across the apex and decurrent on the abaxial face. (Bahia) 1. *P. adenopoda.*
         10. Glands of the stem leaves sessile, 0.2–0.7 mm in diameter; anterior and anterior-lateral staminode glands smooth. (Santa Catarina) 7. *P. catarinensis.*
      9. Glands of the stem leaves borne at the base of the lamina at the costa or halfway on the petiole, or rarely on the petiole just below the lamina.
         11. Each individual umbel 8-flowered, consisting of 4 pairs of flowers, each pair with one pedicel sessile and one pedicel borne on a short primary peduncle (1–2.5 mm long). (Mato Grosso) 21. *P. octoflora.*
         11. Each individual umbel 4-flowered, all pedicels sessile (rarely 1 pedicel in an umbel with a primary peduncle in *P. reticulata*).

12. Anthers of all or of almost all flowers closed. (Minas Gerais, São Paulo, Paraná, southern Goiás, southern and central Mato Grosso, eastern Paraguay, eastern Bolivia) 25. *P. reticulata.*
12. Anthers of all flowers open.
    13. Limb of the lateral petals oblanceolate; petioles of the stem leaves 8–13 mm long; anterior and anterior-lateral staminode glands with an indentation across the apex and decurrent on the abaxial face. (Minas Gerais) 3. *P. andersonii.*
    13. Limb of the lateral petals orbicular, broadly elliptical, or broadly obovate; petioles of the stem leaves 4–20 (–32) mm long; anterior and anterior-lateral staminode glands smooth.
        14. Limb of the lateral petals (4.3–) 5.2–9.5 mm long, (4–) 5–8.5 mm wide; leaves loosely pubescent with T-shaped hairs or loosely tomentose below; lateral umbels always borne on secondary peduncles; all inflorescence leaves petiolate; posterior styles curved toward the anterior-lateral petals; pubescence of the inflorescence axes commonly white (sometimes golden), sparse to moderate (rarely dense). (Minas Gerais, Rio de Janeiro, São Paulo, Paraná) 23. *P. parviflora.*
        14. Limb of the lateral petals 9.5–12.3 mm long, 10–11 mm wide; leaves woolly, tomentose, or sometimes pubescent with T-shaped hairs and tomentose below; lateral umbels sessile or borne on secondary peduncles; all or only the distal inflorescence leaves sessile or subsessile, or sometimes all petiolate; posterior styles inclined toward the posterior-lateral petals; pubescence of the inflorescence axes golden, very dense and obscuring the epidermis. (Minas Gerais) 28. *P. tomentosa.*

8. Terminal inflorescence nodes bearing 4 flowers.
    15. Inflorescence borne on a short axillary shoot (less than 1 cm long), of 1 or 3 umbels; 2° axes less than 5 mm long or absent. (Goiás) 4. *P. axillaris.*
    15. Inflorescence terminal or if axillary borne on a shoot more than 1 cm long, of at least 3 umbels, usually many more (except commonly of 1 or 3 umbels in *P. hispidula*); 2° axes more than 5 mm long.
        16. Anthers of all or of almost all flowers closed.
            17. Leaf glands borne on the surface of the lamina away from the base and the costa, or one or both glands absent; limb of the posterior petal 5.3–7 mm long. (Minas Gerais, Bahia) 22. *P. paludosa.*
            17. Leaf glands borne at the base of the lamina at the costa or halfway on the petiole (sometimes in very large leaves of *P. leptoclada* with a second pair of glands, or rarely only with one pair of glands, borne on the surface of the lamina away from the base and costa); limb of the posterior petal 7.5–12 mm long.
                18. Secondary peduncles absent; inflorescence stipules persistent or sometimes deciduous at the most proximal nodes, large, even the most distal 7–17 mm long; limb of the posterior petal with a capitate-glandular margin. (Minas Gerias, Goiás) 18. *P. leptoclada.*
                18. Secondary peduncles up to 6 mm long or absent; inflorescence stipules usually deciduous but present at the nodes of recently opened flowers, small, the most distal 5–6 mm long or less; limb of the posterior petal with the margin capitate-glandular in the proximal 1/2–4/5, fimbriate-glandular in the distal 1/5–1/2, or sometimes entirely capitate-glandular. (Minas Gerais, São Paulo, Paraná, southern Goiás, southern and central Mato Grosso, eastern Paraguay, eastern Bolivia) 25. *P. reticulata.*
        16. Anthers of all flowers open.
            19. Anthers lacking a glandular connective. (Goiás) 2. *P. anadenanthera.*
            19. Anthers bearing a glandular connective.
                20. All or at least the most distal inflorescence leaves sessile.
                    21. Laminas sericeous below, the hairs sessile or subsessile; base of the lamina cuneate. (Bahia) 26. *P. sericea.*
                    21. Laminas pubescent with T-shaped hairs or tomentose or woolly below, the hairs stalked; base of the lamina cordate or subtruncate.
                        22. Anterior and anterior-lateral staminode glands with an indentation across the apex and decurrent on the abaxial face.

23. Stem leaves sparsely to densely pubescent with T-shaped hairs below; limb of the posterior petal 6.8–8 (–9) mm wide, orbicular or rarely broadly obovate; limbs of the lateral petals with a fimbriate or denticulate margin; posterior-lateral staminode glands 1–1.1 mm long, 0.9–1 mm wide. (Goiás) 12. *P. goiana.*

23. Stem leaves tomentose or woolly below; limb of the posterior petal 4–6.2 mm wide, elliptical or narrowly obovate; limbs of the lateral petals with a fimbriate margin; posterior-lateral staminode glands 1.2–1.4 mm long, 1.1–1.3 mm wide.

24. Anterior and anterior-lateral staminode glands recurved, 1.4–1.6 mm long, 1.3–1.5 mm wide; stem leaves velutinous or tomentulose above, woolly below; anterior style shorter than the posterior two. (Minas Gerais) 8. *P. cipoana.*

24. Anterior and anterior-lateral staminode glands straight, 1.2–1.4 mm long, 1.1–1.3 mm wide; stem leaves velutinous above, tomentose below; styles about equally long. (Minas Gerais) 6. *P. barnebyi.*

22. Anterior and anterior-lateral staminode glands smooth.

25. Hairs of the younger branches and commonly also of the more proximal inflorescence internodes with stalks 0.5 mm or more long (often 1 mm or more long.)

26. Limb of the posterior petal ca 6.5 mm long, ca 5 mm wide, obovate; limbs of the lateral petals 9–9.5 mm long, 8–8.5 mm wide; anterior and anterior-lateral staminode glands equal but larger than the posterior-lateral two; pedicels never arranged around a central glandular mass. (Minas Gerais) 14. *P. hirta.*

26. Limb of the posterior petal ca 8.5 mm long, ca 9 mm wide, orbicular; limbs of the lateral petals 11–11.5 mm long, ca 12 mm wide; all staminode glands equally long, the posterior-lateral two narrower than the anterior and anterior-lateral three; pedicels sometimes arranged around a central glandular mass. (Goiás) 10. *P. gardneri.*

25. Hairs of the stem and inflorescence axes with stalks less than 0.5 mm long.

27. Stem and inflorescence stipules 16–23 mm long, persistent; limbs of the lateral petals 16–16.6 mm long, 15–16 mm wide; posterior styles 5.4–5.5 mm long. (Bahia) 20. *P. megalantha.*

27. Stem stipules 4–13 (–19) mm long, deciduous or sometimes persistent, inflorescence stipules usually smaller, the most distal ca 5–6 mm long or less, deciduous; limbs of the lateral petals 9.6–12 (–15) mm long, 8–12 (–15) mm wide; posterior styles 3.3–4.7 mm long.

28. Limb of the posterior petal 7.5–10 mm long, 6.8–9 mm wide, orbicular or sometimes broadly obovate, ca 2/3–3/4 as wide as the limbs of the lateral petals. (Goiás) 12. *P. goiana.*

28. Limb of the posterior petal 6–7 mm long, 4–5 mm wide, elliptical or slightly obovate, 1/3–1/2 as wide as the limbs of the lateral petals.

29. Limbs of the lateral petals elliptical or obovate, their margins denticulate with the teeth up to 0.3 mm long; anterior style shorter than the posterior two. (Bahia) 5. *P. bahiana.*

29. Limbs of the lateral petals orbicular, their margins fimbriate with the fimbriae up to 0.8 (–1) mm long; styles about equally long. (Minas Gerais) 6. *P. barnebyi.*

20. All inflorescence leaves petiolate.
    30. Anterior and anterior-lateral staminode glands with an indentation across the apex and decurrent on the abaxial face.
        31. Inflorescence commonly of 1 or 3 or 5 umbels, occasionally more, 3° axes absent; anterior and anterior-lateral staminode glands wider than long; limbs of the lateral petals 13–20 mm long. (Coastal regions from Bahia to São Paulo) 15. *P. hispidula.*
        31. Inflorescence of more than 5 umbels, 3° axes usually present; anterior and anterior-lateral staminode glands longer than wide or as long as wide; limbs of the lateral petals 9.5–14 mm long.
            32. Glands of the stem leaves borne on the surface of the lamina away from the base and costa. (Minas Gerais) 27. *P. spinensis.*
            32. Glands of the stem leaves borne at the base of the lamina at the costa.
                33. Petioles of the stem leaves 8–13 mm long; limbs of the lateral petals oblanceolate. (Minas Gerais) 3. *P. andersonii.*
                33. Petioles of the stem leaves 2–5 mm long; limbs of the lateral petals orbicular. (Minas Gerais) 6. *P. barnebyi.*
    30. Anterior and anterior-lateral staminode glands smooth.
        34. Anterior style 5–9.2 mm long, usually strongly arced toward the posterior petal, bearing an oblong stigma at the apex but laterally on the abaxial surface (or rarely with the apex uncinate and bearing a capitate stigma.)
            35. Limbs of the lateral petals 15–17.8 mm long and wide, orbicular; styles 7.3–9 mm long; stem stipules (9.3–) 12–23 mm long. (Goiás, Mato Grosso) 19. *P. magnifica.*
            35. Limbs of the lateral petals 10.5–12 mm long, ca 9–10 mm wide, obovate; styles 5–6.5 mm long; stem stipules ca 6–8 mm long. (Ceará, Piauí, Maranhão, Paraná) 17. *P. jussieuana.*
        34. Anterior style 2.6–5.5 mm long, arced or inclined toward the posterior petal (or rarely toward the anterior sepal) or erect, bearing a capitate stigma, apex never uncinate.
            36. Inflorescence stipules large, even the most distal 7–17 mm long, persistent or sometimes deciduous at the most proximal nodes.
                37. Pedicels commonly arranged around a central glandular mass up to 2.5 mm in diameter; limb of the posterior petal with the margin capitate-glandular in the proximal 1/2–2/3, fimbriate-glandular in the distal 1/3–1/2; anterior style longer than the posterior two; posterior-lateral staminode glands smaller than the anterior and anterior-lateral three. (Mato Grosso, eastern Bolivia) 9. *P. cordistipula.*
                37. Pedicels never arranged around a central glandular mass; limb of the posterior petal with the margin capitate-glandular; anterior style shorter than the posterior two; staminode glands all equally long but the posterior-lateral two narrower than the anterior and anterior-lateral three. (Goiás, Minas Gerais) 18. *P. leptoclada.*
            36. Inflorescence stipules small, the most distal 5–6 mm long or less, usually deciduous but often present at nodes bearing recently opened flowers.
                38. Glands of the stem leaves borne on the surface of the lamina away from the base and costa, or sometimes on some leaves one or both glands absent. (Minas Gerais, Bahia) 22. *P. paludosa.*
                38. Glands of the stem leaves borne at the base of the lamina at the costa or halfway on the petiole.
                    39. Limb of the posterior petal 7.5–10 mm long, 6.8–9 mm wide, orbicular or sometimes broad-

ly obovate, ca 2/3–3/4 as wide as the limbs of the lateral petals; anterior style shorter than the posterior two. (Goiás) 12. *P. goiana.*

39. Limb of the posterior petal 6–7 mm long, 4–5 mm wide, elliptical, ca 1/3–1/2 as wide as the limbs of the lateral petals; styles about equally long. (Minas Gerais) 6. *P. barnebyi.*

1. **Peixotoa adenopoda** C. Anderson, sp. nov. Fig. 12.

Liana. Stipulae vegetativae 7–16 mm longae, acutae vel bifidae, plerumque persistentes. Petioli 4–8 mm longi. Laminae 4.8–9.5 cm longae, 1.3–4.8 cm latae, ellipticae vel parum obovatae vel lanceolatae, rugosae, apice apiculatae vel acuminatae, supra sparsim aureo-velutinae vel sparsim aureo-sericeae, subtus sparsim et laxe aureo-sericeae, ferentes 2 glandulas pedicellatas 1.7–10 mm supra basim 1.2–6 mm a costa. Folia inflorescentiae petiolo brevi, distaliora linearia vel triangularia, apice acuminata vel caudata. Inflorescentia terminalis vel axillaris, umbellis singularibus in nodis subterminalibus, umbellis 3 in nodis terminalibus, pedunculis secundariis 0.5–3 mm longis. Bracteae bracteolaeque praesentes. Pedicelli 11–20 mm longi. Sepala 4–5 mm longa. Limbus petalorum lateralium 10–10.5 mm longus, orbicularis, margine glanduloso-fimbriato. Limbus petali postici ca 6 mm longus, ellipticus vel anguste obovatus, margine glandulis capitatis ornato. Glandulae 3 staminodiorum anticorum apice profunde indentatae, indentatione in pagina abaxiali decurrenti. Styli subaequales vel anticus brevior, 2.8–3.6 mm longi, anticus parum arcuatus versus petalum posticum, postici divergentes, inclinati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Vine. Vegetative branches purplish-brown, velutinous, pubescence abraded from older parts. Stem stipules 7–16 mm long, 7.6–17 mm wide, cordate, entire with the apex acute, or bifid, glabrous or finely, sometimes sparsely, velutinous or tomentulose adaxially, appressed sericeous abaxially, usually persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 5 mm long, 3 mm wide, commonly persistent. Stem leaves with the petiole 4–8 mm long, densely and loosely golden velutinous, laminas 4.8–9.5 cm long, 1.3–4.8 cm wide, elliptical or slightly obovate to lanceolate, apex apiculate or in the narrower acuminate, base cordate or almost truncate, rugose, sparsely golden velutinous-sericeous above, sparsely golden sericeous below, a pair of stalked glands borne on the surface of the lamina, 1.7–10 mm above the base, 1.2–6 mm from the costa, each gland 0.8–1.5 mm in diameter, stalk 0.8–1 mm high. Inflorescence leaves with the petiole ca 1 mm or more long, laminas abruptly smaller than the cauline, the smallest 1.3 mm long, 0.7 mm wide, the most proximal elliptical or linear-lanceolate, the more distal narrowly triangular or linear, apex acuminate or caudate, sparsely sericeous or glabrous above, sparsely sericeous below, a pair of glands at or near the base at or near the costa, each gland 0.5–1 mm in diameter, the glands stalked in the most proximal, sessile in the more distal. Inflorescence terminal or axillary, the axes loosely sericeous or velutinous, internodes of the primary axis 0.6–3.5 cm long, 2° axes 1–6 cm long, 3° axes 6.5–12 mm long, subsidiary axes absent, at the more distal nodes the 2° and 3° axes usually suppressed, with 1 or 2 umbels sessile or borne on secondary peduncles in the leaf axil, always with 3 umbels at the terminal nodes, or occasionally with only 1 umbel at the terminal node of a 3° axis, each umbel 4-flowered, primary peduncles absent, secondary peduncles up to 3 mm long or absent. Bracts 0.5–1 mm long, 0.2–0.6 mm wide, triangular, glabrous or very sparsely velutinous on both surfaces and on the margins; bracteoles 0.1–0.3 mm long and wide, oblong, triangular or semicircular,

glabrous, sometimes the margins velutinous. Pedicels 11–20 mm long, velutinous. Sepals 4–5 mm long, 1.3–2 mm wide, adaxially very sparsely velutinous or tomentulose, more densely so near the apex, glands 1.2–1.5 mm long. Claw of the lateral petals ca 2 mm long, limb 10–10.5 mm long and wide, orbicular, base attenuate, fimbriae up to 0.3 mm long, glandular, claw of the posterior petal 4–4.3 mm long, limb ca 6 mm long, ca 4 mm wide, elliptical or narrowly obovate, fimbriae up to 0.4 mm long, capitate-glandular. Filaments of the lateral stamens 3.4–3.6 mm long, posterior filament 2.5–2.6 mm long, arced toward the posterior petal, anthers 1.1–1.2 mm long, glandular connectives ca 0.5 mm long. Pollen grains ca 42 μm. Filaments of the anterior staminode 4–4.2 mm long, anterior-lateral filaments 3.3–3.7 mm long, posterior-lateral filaments 2.6–2.8 mm long, inflexed between the posterior styles, anterior and anterior-lateral glands ca 1.2 mm long and wide, posterior-lateral glands ca 1.1 mm long, 0.9–1 mm wide, anterior and anterior-lateral glands with a deep indentation across the apex and decurrent on the abaxial face, posterior-lateral glands smooth. Styles 2.8–3.6 mm long, anterior styles ca 0.4 mm wide, sometimes shorter but always a little stouter than the posterior two, slightly curved toward the posterior petal, posterior styles ca 0.3 mm wide, strongly divergent, inclined toward the posterior-lateral petals, all styles velutinous in the proximal 1/3 of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Samara not seen.

Type. *Jesus 392*. Brazil. Bahia: Maracás, saida de Itiruçu, 20 May 1969 (holotype CEPEC, isotype MICH).

Paratype. *Pinheiro 1870*. Brazil. Bahia: Rod. Itiruçu-Maracás, 8 July 1972 (CEPEC, MICH).

Peixotoa adenopoda is known only from the type and the paratype (Fig. 3). It is one of four species in which the terminal inflorescence nodes bear three umbels and thus are 12-flowered. It is readily distinguished from the other three by its stalked leaf glands which are borne on the surface of the lamina away from the base and either away from the costa or adjacent to it. The leaf glands of *P. catarinensis*, *P. parviflora*, and *P. tomentosa* are sessile. None of these species

FIG. 3. Distribution of *P. adenopoda*, *P. anadenanthera*, *P. andersonii*, and *P. axillaris*.

occurs in Bahia. The only other species with stalked but basal leaf glands is the glabrous *P. hatschbachii* of south-central Goiás. *P. adenopoda* is also unusual in that its leaves are sericeous. *P. sericea,* also from Bahia, is the only other species in the genus with sericeous leaves. It has sessile leaf glands, and its terminal inflorescence nodes bear a single umbel, i.e., are 4-flowered.

2. Peixotoa anadenanthera C. Anderson, sp. nov. Fig. 13.

Frutex pauciramosus usque ad 1.5 m. Caules dense aureo-velutini. Stipulae vegetativae 7.3–7.5 mm longae, anguste triangulares, deciduae. Petioli 2.5–6 mm longi. Laminae 7–11 cm longae, 3.2–5.3 cm latae, anguste ellipticae vel lineari-lanceolatae, supra aureo-velutinae, subtus aureo-tomentosae, basi costae biglandulosae vel glandulis apice petioli. Folia inflorescentiae petiolo brevi vel sessilia, linearia vel subulata, distaliora decurrentia, petiolis basi biglandulosis. Inflorenscentia axillaris, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 11–26 mm longi. Sepala ca 5.2 mm longa. Limbus petalorum lateralium 9.5–ca 10 mm longus, late obovatus, margine glanduloso-fimbriato. Limbus petali postici 6.2–6.5 mm longus, obovatus, margine ¾ proximalibus glandulis capitatis ornato, ¼ distali fimbriato vel denticulato, glanduloso vel eglanduloso. Antherae sine connectivo glanduloso. Stylus anticus 3.3–3.5 mm longus, erectus vel parum inclinatus versus petalum posticum, styli postici 3.6–4 mm longi, parum divergentes, parum inclinati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Little-branched shrub to 1.5 m. Vegetative branches densely golden velutinous, pubescence abraded from older parts. Stem stipules 7.3–7.5 mm long, 4–6.5 mm wide, narrowly triangular, apex acute, tomentulose to glabrate adaxially, densely tomentulose-velutinous abaxially, deciduous; inflorescence stipules like the cauline, sometimes smaller, the smallest not less than 3.6 mm long, 3.5 mm wide, persistent (?). Stem leaves with the petiole 2.5–6 mm long, densely velutinous, laminas 7–11 cm long, 3.2–5.3 cm wide, narrowly elliptical or linear-lanceolate, apex apiculate, base truncate, rugose, golden velutinous above, golden tomentose below, a pair of sessile glands hidden in the dense pubescence halfway on the petiole or on the petiole up to 1 mm below the lamina, each gland 0.6–1.2 mm in diameter, or sometimes the glands absent. Inflorescence leaves with a petiole 3.5 mm or less long, or subsessile or sessile, laminas abruptly smaller than the cauline, the smallest not less than 2.5 mm long, 0.1 mm wide, linear to subulate, apex acute or acuminate, the petiolate with the base decurrent, tomentulose and pubescent with T-shaped hairs above, densely tomentulose-velutinous below, a pair of glands at the base of the petiole in petiolate leaves, at the base of the lamina at the costa in sessile leaves, each gland 0.4–0.7 mm in diameter. Inflorescence terminal or axillary, internodes of the primary axis 0.9–5.8 cm long, mature secondary axes not seen, tomentulose-velutinous, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.8–1.1 mm long, ca 0.3 mm wide, narrowly triangular, glabrous; bracteoles ca 0.3 mm long, ca 0.2 mm wide, triangular, glabrous. pedicels 11–26 mm long, densely tomentulose-velutinous. Sepals ca 5.2 mm long, ca 2.3 mm wide, adaxially the proximal ⅓ glabrous, the distal ⅔ tomentulose, glands 1.8–2.2 mm long, 0.8–1.1 mm wide. Claw of the lateral petals 2–2.5 mm long, limb 9.5–10 mm long and wide, broadly obovate, base briefly attenuate, margin irregularly fimbriate-denticulate, fimbriae/teeth up to 0.5 mm long, glandular. Claw of the posterior petal 3.5–4 mm long, limb 6.2–6.5 mm long, 5.2–5.5 mm wide, obovate, fimbriae up to 0.4 mm long, those of the proximal ¾ capitate-glandular, the distal ¼ fimbriate-denticulate, glandular or eglandular. Filaments of the anterior-lateral and the posterior stamens 3.2–3.5 mm long, posterior filament slightly curved toward the posterior petal,

posterior-lateral filaments 3.6–3.7 mm long, anthers 1.5–1.7 mm long, glandular connectives absent. Pollen grains ca 50 μm. Filaments of the anterior and the posterior-lateral staminodes 3.1–3.3 mm long, posterior-lateral filaments inflexed between the posterior styles, anterior-lateral filaments 3.5–3.6 mm long, anterior gland ca 1.4 mm long and wide, anterior-lateral glands 1.2–1.3 mm long, ca 1.2 mm wide, posterior-lateral glands 1–1.1 mm long, ca 1 mm wide, all glands with the apex and abaxial face smooth. Anterior style 3.3–3.5 mm long, ca 0.4 mm wide, erect or slightly curved toward the posterior petal, sometimes with a few scattered hairs in the proximal ¼ of its length, posterior styles 3.6–4 mm long, ca 0.3 mm wide, somewhat divergent, slightly inclined toward the posterior-lateral petals, glabrous, stigmas 0.4–0.5 mm in diameter, capitate. Samara not seen.

Type. *Hatschbach 36904*. Brazil. Goiás: GO–12, 30 km S of Cavalcante, 26 May 1975 (holotype MBM, isotype MICH).

Peixotoa anadenanthera is known only from the type (Fig. 3). It is unique in that its anthers lack the glandular connectives. It also differs from most other species in that the stem stipules are narrow, and in that the leaves tend to be narrowly elliptical. The internodes of the younger branches and branchlets are densely velutinous. The hairs are similar to those of *P. hirta* and *P. gardneri* in that the stalk is usually more than 0.5 mm long.

3. Peixotoa andersonii C. Anderson, sp. nov. Fig. 14.

Caules procumbentes usque ad 4 m. Stipulae vegetativae 7–11 mm longae, triangulares, acutae vel bifidae, persistentes. Petioli 8–13 mm longi. Laminae 6.7–15.3 cm longae, 3.3–7.9 cm latae, anguste ellipticae, supra aureo-velutinae, subtus aureo-tomentosae, basi juxta costam biglandulosae. Folia inflorescentiae petiolo brevi vel sessilia, lineari-lanceolata vel anguste triangularia vel subulata. Inflorescentia terminalis, umbellis singularibus, interdum ramis secundariis nodorum distalissimorum multum redactis. Bracteae bracteolaeque praesentes. Pedicelli 16–23 mm longi. Sepala (3.8–)4–5.5 mm longa. Limbus petalorum lateralium 12.5–14 mm longus, oblanceolatus, decurrens, margine glanduloso-fimbriato. Limbus petali postici ca 6 mm longus, subrectangularis, margine ⅔ proximalibus glandulis capitatis ornato, ⅓ distali glanduloso-fimbriato. Glandulae 3 staminodiorum anticorum apice profunde indentatae, indentatione in pagina abaxiali decurrenti. Stylus anticus 4.1–4.3 mm longus, arcuatus versus petalum posticum, styli postici 4.4–4.6 mm longi, parum divergentes, parum inclinati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Stems procumbent, up to 4 m. Vegetative branches golden velutinous, pubescence abraded from older parts. Stem stipules 7–11 mm long, 7–10.6 mm wide, triangular, entire with the apex acute, or bifid, finely tomentulose adaxially, tomentulose-sericeous abaxially, persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 3.2 mm long and wide, the most distal sometimes split into two narrow lobes, persistent. Stem leaves with the petiole 8–13 mm long, densely golden velutinous, laminas 6.7–15.3 cm long, 3.3–7.9 cm wide, narrowly elliptical, apex apiculate, base usually truncate, rarely cordate, golden velutinous above, golden tomentose below, a pair of sessile glands at the base at the costa, each gland (1–) 1.5–2.5 mm in diameter. Inflorescence leaves with the petiole 1 mm or more long or the most distal sessile, laminas abruptly smaller than the cauline, the smallest not less than 1.8 mm long, 0.6 mm wide, linear-lanceolate or narrowly triangular or subulate, apex acuminate, sparsely tomentulose above, densely velutinous-tomentulose below, a pair of glands at the base at the costa, these sometimes fused, each gland 0.7–1.2 mm in diameter, sometimes with a second, smaller pair (ca 0.4 mm in diameter) just below the larger pair; rarely the most

distal leaves reduced to sessile, linear or subulate, eglandular bracts, or rarely the most distal nodes bearing split stipules, the leaves absent. Inflorescence terminal or axillary, the axes densely golden velutinous, internodes of the primary axis 2.8–6.5 cm long, 2° axes 2.1–6.1 cm long, 3° axes 0.5–1.1 cm long, subsidiary axes absent, sometimes the most distal axes much reduced; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.5–0.8 mm long, 0.2–0.3 mm wide, narrowly triangular, glabrous; bracteoles 0.1–0.2 mm long and wide, linear, glabrous. Pedicels 16–23 mm long, densely golden velutinous. Sepals (3.8–) 4–5.5 mm long, 2–2.3 mm wide, adaxially the proximal ½ glabrous, the distal ½ tomentulose, glands 1.4–1.9 mm long, 0.8–1.1 mm wide. Claw of the lateral petals 1.6–2 mm long, limb 12.5–14 mm long, 9–11 mm wide, oblanceolate, base decurrent, fimbriae up to 0.5 mm long, glandular. Claw of the posterior petal 3.7–4 mm long, limb ca 6 mm long, 4–4.6 mm wide, subrectangular, fimbriae up to 0.4 mm long, those of the proximal ⅔ capitate-glandular, the distal ⅓ fimbriate-glandular. Filaments of the lateral stamens 3.6–4 mm long, posterior filament ca 3 mm long, strongly arced toward the posterior petal, anthers 1.2–1.3 mm long, glandular connectives 0.6–0.7 mm long. Pollen grains ca 50 μm. Filament of the anterior and anterior-lateral staminodes 3.6–3.8 mm long, the anterior filament often a little longer than the anterior-lateral two, posterior-lateral filaments 3.2–3.3 mm long, inflexed between the posterior styles, anterior and anterior-lateral glands 1.4–1.5 mm long, 1.3–1.4 mm wide, posterior-lateral glands 1.1–1.2 mm long, ca 1.1 mm wide, anterior and anterior-lateral glands with a deep indentation across the apex and decurrent on the abaxial face, posterior-lateral glands smooth. Anterior style 4.1–4.3 mm long, 0.3–0.4 mm wide, arced toward the posterior petal, posterior styles 4.4–4.6 mm long, 0.3—0.4 mm wide, slightly divergent, slightly curved toward the posterior-lateral petals, all styles with scattered hairs in the proximal ⅓ of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Samara not seen.

Type. *Anderson 11591*. Brazil. Minas Gerais: Mun. Diamantina, steep-sided valley of Biribiri, 1100 m, 25 Feb 1975 (holotype MICH, isotype NY).

Peixotoa andersonii is known only from the type (Fig. 3). It forms procumbent stems up to 4 m long which bear erect inflorescences, an unusual habit in this genus. It is unique in that the limbs of the lateral petals are oblanceolate and decurrent on the claw. The anterior and anterior-lateral staminode glands have a deep indentation across the apex and decurrent on the abaxial face. This species is also unusual in that the stem leaves have a petiole at least 8 mm long. Vegetatively it resembles *P. parviflora* and the less densely pubescent forms of *P. tomentosa*. These two species have smooth staminode glands and lateral petals whose limbs are usually orbicular or sometimes elliptical or broadly ovate. They are also distinguished by their inflorescences, in which the terminal node bears three umbels and is thus 12-flowered. In *P. andersonii* the terminal nodes bear one umbel, i.e., are 4-flowered. However, sometimes at some terminal nodes the 2° axes are greatly reduced, the stipules are split into several, often lacerate, strips, and the inflorescence leaves are absent. With such an arrangement the inflorescence branches resemble those of *P. parviflora* and *P. tomentosa*.

This species is named for my husband, William R. Anderson, an expert student of the Malpighiaceae, to whom I am much indebted.

4. Peixotoa axillaris C. Anderson, sp. nov. Fig. 15

Frutex usque ad 1 m. Stipulae vegetativae 10.7–11.5 mm longae, triangulari-cordatae, acutae, deciduae. Petioli 4–8 mm longi. Laminae 7.1–13.4 cm longae, 5.5–9 cm latae, ellipticae vel ovatae vel suborbiculatae, supra velutinae, subtus tomentosae, basi juxta costam biglandulosae. Folia inflorescentiae petiolo brevi vel sessilia, elliptica vel linearia vel subulata. Inflorescentia ex 1–3 umbellis

ramo axillari brevi (2–9 mm longo) constans, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 10–13 mm longi. Sepala 4.2–4.7 mm longa. Limbus petalorum lateralium 12.5–13 mm longus, late obovatus, margine glanduloso-fimbriato. Limbus petali postici ca 10 mm longus, obovatus, margine ⅓ proximali glandulis capitatis ornato, ⅔ distalibus glanduloso-fimbriato. Filamenta staminum subaequalia. Styli subaequales, 4.4–4.6 mm longi, anticus erectus, postici divergentes, parum inclinati versus petala postico-lateralia; stigmata capitata. Ala dorsalis samarae 2.7–2.9 cm longa, 1.9–2 cm lata, alae laterales 4.6–5 mm latae, 10–11 mm altae.

Shrub ca 1 m tall. Vegetative branches velutinous-tomentulose. Stem stipules 10.7–11.5 mm long, ca 11 mm wide, triangular-cordate, apex acute, adaxially glabrous or the proximal ½ finely tomentulose, the distal ½ glabrous, abaxially tomentulose-velutinous, deciduous; inflorescence stipules like the cauline but smaller, the smallest not less than 4.2 mm long, 5 mm wide, cordate, concave, deciduous. Stem leaves with the petiole 4–8 mm long, densely golden velutinous, laminas 7.1–13.4 cm long, 5.5–9 cm wide, elliptical or ovate or suborbicular, apex apiculate, base cordate, velutinous above, tomentose below, a pair of sessile glands at the base at the costa, each gland 1.1–1.6 mm in diameter. Inflorescence leaves with the petiole up to 1.5 mm long or sessile, laminas abruptly smaller than the cauline, the smallest not less than 3.8 mm long, 0.8 mm wide, elliptical or linear or subulate, apex acuminate, glabrous above, densely velutinous-tomentulose below, a pair of glands at the base at the costa, each gland 0.6–0.8 mm in diameter. Inflorescence borne on a short (2–9 mm long) axillary shoot, the terminal umbel sessile or borne on a primary axis, 1–6.5 mm long, solitary or with two lateral sessile umbels, or with a pair of 2° axes 3–3.5 mm long, each bearing one umbel, subsidiary axes absent; umbels 4-flowered, primary and secondary peduncles absent. Bracts 0.6–0.7 mm long, ca 0.7 mm wide, triangular or semicircular, glabrous, sometimes with scattered hairs abaxially and/or on the margins; bracteoles 0.2–0.6 mm long, 0.2–0.3 mm wide, triangular or narrowly so, glabrous, often with scattered hairs on the margins. Pedicels 10–13 mm long, velutinous, up to ½ again as long in fruit. Sepals 4.2–4.7 mm long, 2.5–2.6 mm wide, adaxially the proximal ¼ glabrous, the distal ¾ tomentulose, glands 1.5–1.7 mm long, 0.8–0.9 mm wide. Claw of the lateral petals 1.7–2 mm long, limb ca 12.5–13 mm long, ca 11.5–12 mm wide, broadly obovate, base attenuate, fimbriae up to 0.6 mm long, glandular. Claw of the posterior petal ca 5 mm long, limb ca 10 mm long, ca 9 mm wide, obovate, fimbriae up to 0.6 mm long, those of the proximal ⅓ capitate-glandular, the distal ⅔ fimbriate-glandular. Stamen filaments 4.2–4.5 mm long, posterior filament usually a little shorter than the lateral four, very slightly curved toward the posterior petal, anthers 1.5–1.8 mm long, glandular connectives 0.8–1 mm long. Pollen grains 57–66 μm. Filament of the anterior staminode ca 5.2 mm long, anterior-lateral and posterior-lateral filaments 4.8–4.9 mm long, the posterior-lateral two inflexed between the posterior styles, all glands 1.4–1.5 mm long, anterior and anterior-lateral glands 1.2–1.3 mm wide, posterior-lateral glands ca 1 mm wide, all glands with the apex and abaxial face smooth. Styles 4.4–4.6 mm long, 0.3–0.4 mm wide, anterior style usually a little longer and stouter than the posterior two, erect, posterior styles divergent, slightly inclined toward the posterior-lateral petals, all styles glabrous, anterior stigma ca 0.6 mm in diameter, posterior stigmas ca 0.5 mm in diameter, all stigmas capitate. Carpophore up to 3.5 mm long. Torus up to 5.5 mm high. Samara with the dorsal wing 2.7–2.9 cm long, 1.9–2 cm wide, upper margin gently sigmoid, lower margin arced, erose, lateral wings 4.6–5 mm wide, 10–11 mm high, rectangular, areole 5–6 mm long, 6–6.6 mm wide, nut 7–7.5 mm long, 4–5.4 mm in diameter, seed ca 8.5 mm long, outer cotyledon ca 11 mm long, ca 3.2 mm wide, folded at ca ⅓ of its length, inner cotyledon ca 5.6 mm long, ca 2.3 mm wide, straight.

Type. *Irwin & Soderstrom 7443*. Brazil. Goiás: Serra de Caiapó, 17°12′S, 51°47′W, ca 60 km S of Caiapônia on road to Jataí, 800–1000 m, 27 Oct 1964 (holotype UB, isotypes MICH, NY).

Peixotoa axillaris is known only from the type (Fig. 3). It is readily distinguished by its reduced inflorescence, borne on a short axillary shoot, which is composed of one or three umbels. The terminal umbel may be sessile or borne on a tiny primary axis. The lateral umbels are sessile. The type is apparently an apomict. The closed anthers contain pollen that is mostly aborted and 88–91% non-staining in cotton blue in lactophenol.

The coastal *P. hispidula* is the only other species whose inflorescences may consist of only one or three umbels, but these are never sessile. It is commonly glabrous or only very sparsely pubescent. The limbs of its lateral petals are 13–20 mm long, while the limb of its posterior petal is only 6.5–8.2 mm long. The staminode glands are strongly dimorphic. The anterior and anterior-lateral three have an indentation across the apex and decurrent on the abaxial face. *P. axillaris* is pubescent in all its vegetative parts. The limb of the posterior petal (ca 10 mm long) is only a little smaller than the limbs of the lateral petals (12.5–13 mm long). The staminode glands are subequal and smooth.

5. Peixotoa bahiana C. Anderson, sp. nov. Fig. 14.

Frutex usque ad 2.5 m. Stipulae vegetativae 7.5–13 mm longae, acutae vel bifidae, deciduae. Petioli 2.5–4 mm longi. Laminae 4.5–6.5 cm longae, 2.8–3.8 cm latae, anguste ellipticae vel anguste ovatae, rugosae, supra velutinae, subtus in venis tomentosae, basi juxta costam biglandulosae. Folia inflorescentiae sessilia, subulata. Inflorescentia terminalis, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli (13–)18–23 mm longi. Sepala 4.5–5.8 mm longa. Limbus petalorum lateralium 11–12.3 mm longus, obovatus vel ellipticus, denticulatus, glandulosus vel eglandulosus. Limbus petali postici 6.2–7 mm longus, ellipticus vel parum obovatus, margine glandulis capitatis ornato. Stylus anticus 3.4–3.6 mm longus, erectus, styli postici 4.2–4.3 mm longi, erecti, parum divergentes; stigmata capitata. Samara ignota.

Shrub up to 2.5 m. Vegetative branches finely tomentulose-velutinous. Stem stipules 7.5–13 mm long, ca 9–13 mm wide, cordate, entire with the apex acute, or bifid, finely and sparsely velutinous or velutinous-tomentulose adaxially, densely velutinous-tomentulose abaxially, deciduous; inflorescence stipules like the cauline, usually a little smaller, deciduous. Stem leaves with the petiole 2.5–4 mm long, densely velutinous, laminas 4.5–6.5 cm long, 2.8–3.8 cm wide, narrowly elliptical or narrowly ovate, apex apiculate, base cordate, rugose, velutinous above, tomentose especially on the veins below, a pair of sessile glands at the base at the costa, each gland 0.8–1.6 mm in diameter. Inflorescence leaves of the first and sometimes second node of the primary axis petiolate, the others sessile, laminas abruptly smaller than the cauline, the smallest not less than 4.6 mm long, 0.8 mm wide, the most proximal linear-lanceolate, the more distal subulate, apex acuminate, glabrous above, velutinous-tomentulose below, a pair of glands at the base at the costa, each gland 0.7–1.5 mm in diameter, sometimes with a second, smaller pair (0.3–0.6 mm in diameter) above or below the larger pair. Inflorescence terminal, the axes velutinous or velutinous-tomentulose, internodes of the primary axis 1.2–6.5 cm long, 2° axes 2.9–4.5 cm long, 3° axes 2.2–5.8 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 1–1.2 mm long, 0.7–1.1 mm wide, oblong, with a few scattered hairs on both surfaces and along the margin; bracteoles ca 0.2 mm long, 0.1–0.2 mm wide, oblong or triangular, glabrous. Pedicels (13–) 18–23 mm long, velutinous. Sepals 4.5–5.8 mm long,

2.5–2.7 mm wide, adaxially glabrous or tomentulose only in the distal 1/5, glands 1.8–2.2 mm long, 0.9–1.2 mm wide. Claw of the lateral petals 2–2.3 mm long, limb 11–12.3 mm long, 8–11.1 mm wide, obovate or elliptical, base briefly attenuate or truncate, denticulate, the teeth up to 0.3 mm long, glandular or eglandular. Claw of the posterior petal 4–4.3 mm long, limb 6.2–7 mm long, 4.1–4.2 mm wide, elliptical or slightly obovate, fimbriae up to 0.4 mm long, capitate-glandular. Filaments of the lateral stamens 4–4.2 mm long, posterior filament 3.2–3.6 mm long, arced toward the posterior petal, anthers 1.2–1.5 mm long, glandular connectives 0.7–1 mm long. Pollen grains 42–50 μm. Filaments of the anterior and anterior-lateral staminodes 4–4.2 mm long, posterior filaments 3.3–3.6 mm long, slightly curved toward the posterior styles, anterior and anterior-lateral glands 1.1–1.2 mm long and wide, posterior-lateral glands 0.8–1 mm long, 0.7–0.8 mm wide, all glands with the apex and abaxial face smooth. Anterior style 3.4–3.6 mm long, ca 0.4 mm wide, erect or very slightly curved toward the posterior petal, posterior styles 4.2–4.3 mm long, ca 0.3 mm wide, slightly divergent, erect, all styles with some scattered hairs in the proximal ¼ (rarely ⅓) of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Samara not seen.

Type. *Irwin et al. 14889*. Brazil. Bahia: Drainage of the Rio Corrente, ca 5 km S of Rio Roda Velha, ca 150 km SW of Barreiras, 900 m, 15 Apr 1966 (holotype UB, isotypes MICH, NY).

Paratype. *Davidse et al. 12208*. Brazil. Bahia: 39 km NE of the Goiás-Bahia border along Highway BR–020, 930 m, 8 April 1976 (MO).

This species is known only from the type and paratype (Fig. 4). In *P. bahiana* the narrowly elliptical leaves are tomentose below, the inflorescence leaves are

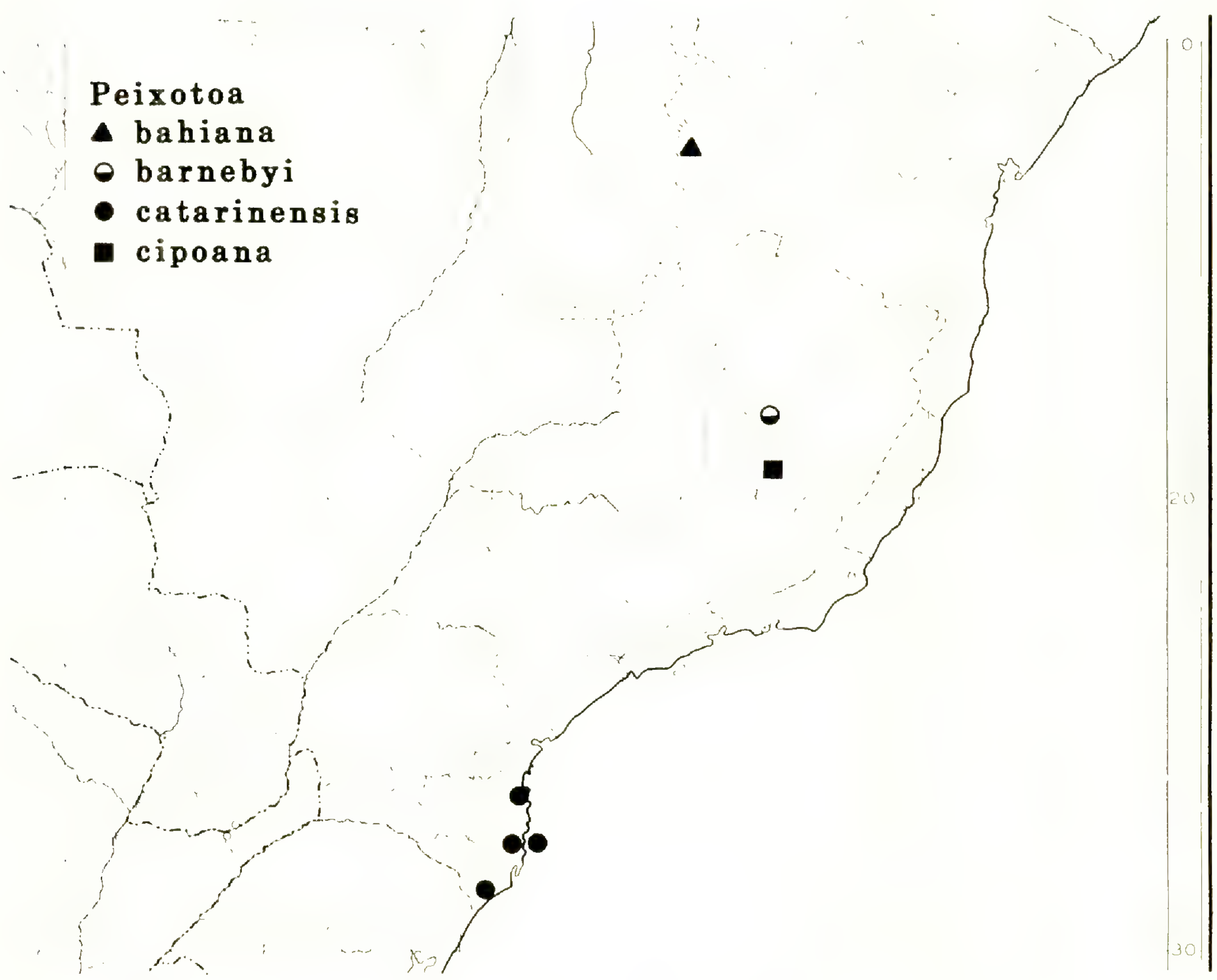

FIG. 4. Distribution of *P. bahiana*, *P. barnebyi*, *P. catarinensis*, and *P. cipoana*.

sessile, and the stipules are deciduous. The elliptical or slightly oblong limb of the posterior petal is relatively small. The margins of the limbs of the lateral petals are denticulate. *P. bahiana* is readily distinguished from the other three relatively small-flowered species that are known from Bahia. *P. adenopoda* and *P. sericea* are both reported from the more eastern part of the state. *P. adenopoda* is recognized by the stalked leaf glands that are borne on the surface of the blade away from the costa and base, and *P. sericea* by the sericeous vesture of its leaves. In *P. bahiana* the leaf glands are sessile and borne at the base at the costa. *P. paludosa* also bears the leaf glands on the surface of the lamina rather than at the base, and has petiolate inflorescence leaves. The inflorescence stipules are often persistent at the more distal nodes.

6. Peixotoa barnebyi C. Anderson, sp. nov. Fig. 16.

Caules usque ad 1.5 m. Stipulae vegetativae 6.5–12 mm longae, acutae vel plerumque bifidae, plerumque persistentes. Petioli 2–5 mm longi. Laminae 5.3–10.7 cm longae, 2.5–7.5 cm latae, anguste vel late ellipticae, ovatae vel suborbiculares, supra velutinae, subtus dense tomentosae, basi juxta costam biglandulosae. Folia inflorescentiae petiolo brevi, distaliora subsessilia, lanceolata vel linearia. Inflorescentia terminalis, umbellis singularibus. Bracteae bracteolaeque praesentes vel interdum absentes. Pedicelli 12–25 mm longi. Sepala (4–)4.5–5.2 mm longa. Limbus petalorum lateralium 11–13.5 mm longus, orbicularis, margine fimbriato, glanduloso vel eglanduloso. Limbus petali postici 6–7 mm longus, ellipticus, margine glandulis capitatis ornato. Glandulae staminodiorum apice indentatae, indentatione in pagina abaxiali decurrenti. Styli subaequales, 3.8–4.1 mm longi, anticus posticis semper brevior, erectus vel parum inclinatus versus sepalum anticum, postici divergentes, arcuati versus petala postico-lateralia; stigmata capitata. Samaram maturam non vidi.

Shrub to 1.5 m. Vegetative branches purplish-brown, tomentulose. Stem stipules 6.5–12 mm long, 9–12 mm wide, cordate, commonly bifid, sometimes entire with the apex acute, rarely split almost to the base, sparsely tomentulose or glabrate adaxially, tomentose-velutinous abaxially, usually persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 3.5 mm long, 3.2 mm wide, glabrous or sparsely velutinous adaxially, tomentulose or tomentulose-velutinous abaxially, deciduous. Stem leaves with the petiole 2–5 mm long, densely velutinous-tomentose, laminas 5.3–10.7 cm long, 2.5–7.5 cm wide, narrowly to broadly elliptical or ovate or suborbicular, apex apiculate, base cordate, velutinous above, densely tomentose below, a pair of sessile glands at the base at the costa or halfway on the petiole, each gland 1–1.9 mm in diameter. Inflorescence leaves with a short petiole at the more proximal nodes, the most distal subsessile or sessile, laminas abruptly smaller than the cauline or gradually decreasing in size toward the distal nodes, the smallest not less than 1.2 mm long, 0.8 mm wide, lanceolate or linear, velutinous above, densely velutinous-tomentulose below, a pair of glands halfway on the petiole, each gland (0.4–) 0.7–1.8 mm in diameter. Inflorescence terminal, the axes tomentulose, internodes of the primary axis 2.7–10.8 mm long, 2° axes 3.4–9.6 cm long, 3° axes (0.5–) 2–4.8 cm long, mature 4° axes not seen, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary peduncles absent, secondary peduncles rare, up to 1.5 mm long. Bracts 0.7–1.3 mm long, 0.3–0.5 mm wide, triangular, glabrous; bracteoles 0.1–0.4 mm long and wide, broadly triangular, glabrous; sometimes bracts and bracteoles absent. Pedicels 12–25 mm long, tomentose. Sepals (4–) 4.5–5.2 mm long, 2–3.1 mm wide, adaxially the proximal ⅓–½ glabrous, the distal ½–⅔ tomentulose, glands 1.6–2.1 mm long, 0.8–1.3 mm wide. Claw of the lateral petals 2–2.5 mm long, limb 11–13.5 mm long, 11–13.8 mm wide, orbicular, base attenu-

ate, fimbriae up to 0.8 (–1) mm long, glandular or eglandular. Claw of the posterior petal 4.5–5 mm long, limb 6–7 mm long, 4–4.5 mm wide, elliptical, fimbriae up to 0.5 mm long, capitate-glandular. Filaments of the lateral stamens 4–4.5 mm long, posterior filament 3.3–3.5 mm long, arced toward the posterior petal, anthers 1.3–1.5 mm long, glandular connectives 0.8–0.9 mm long. Pollen grains ca 50 μm. Filaments of the anterior stamiode 3.9–4.7 mm long, always exceeding the anterior-lateral two, anterior-lateral filaments 3.7–4.3 mm long, always exceeding the posterior-lateral two, posterior-lateral filaments 3.5–4 mm long, inflexed between the posterior styles, glands 1.2–1.4 mm long, 1.1–1.3 mm wide, the posterior two often a little narrower than the anterior three, all glands with an indentation across the apex and decurrent on the abaxial face, the indentation sometimes very shallow in the posterior-lateral two. Styles 3.8–4.1 mm long, anterior style ca 0.3 mm wide, always a little stouter than the posterior two, erect or slightly inclined toward the anterior sepal, posterior styles ca 0.2 mm wide, divergent, arced toward the posterior-lateral petals, all styles glabrous, stigmas ca 0.4 mm in diameter, capitate. Mature samara not seen.

Type. *Anderson 8623*. Brazil. Minas Gerais: Serra do Espinhaço, 30 km by road SW of Gouvêia, at KM 60 on road to Curvelo, 1150 m, 11 Apr 1973 (holotype UB, isotypes MICH, NY).

Paratype. *Anderson 11537*. Brazil. Minas Gerais: Mun. Gouvêia, ascent of Serra do Espinhaço, on BR–259, 860–1000 m, 23 Feb 1975 (MBM, MICH).

Peixotoa barnebyi is known only from the type and paratype (Fig. 4). It is one of three species, all from the Serra do Espinhaço, in which all five staminode glands have an indentation across the apex and decurrent on the abaxial face. In the posterior-lateral glands the indentation may be quite shallow and difficult to detect. *P. spinensis* differs in that the leaf glands are borne on the surface of the blade away from the base and costa. In *P. cipoana* the unusually large staminode glands are recurved. In both species the posterior styles exceed the anterior one. In *P. barnebyi* the leaf glands are borne at the base at the costa, the staminode glands are erect, and the styles are subequal. Mature fruits have not been seen. However, the immature samaras of *Anderson 8623* are similar to those of *P. parviflora* and *P. tomentosa*.

This species is named for Rupert C. Barneby, a distinguished authority on many groups of plants.

7. Peixotoa catarinensis C. Anderson, sp. nov. Fig. 17.

Frutex volubilis. Stipulae vegetativae et inflorescentiae 4.5–ca 9 mm longae, deciduae. Petioli 4.5–15 mm longi. Laminae 3–10.2 cm longae, 2.2–7.6 cm latae, late vel anguste ellipticae interdum ovatae vel obovatae interdum lanceolatae, basi cordatae interdum sinu truncato, supra velutinae, subtus sericeae vel tomentosae, biglandulosae 1.2–9.8 mm supra basim 2.3–6.5 mm a costa. Folia inflorescentiae petiolo brevi. Inflorescentia terminalis vel axillaris, umbellis singularibus in nodis subterminalibus, umbellis 3 in nodis terminalibus, pedunculis secundariis ca 1–13 mm longis. Bracteae bracteolaeque praesentes. Pedicelli 18–25 mm longi. Sepala 4.2–5 mm longa. Limbus petalorum lateralium 11–12 mm longus, orbicularis, margine glanduloso-fimbriato. Limbus petali postici 8.5–9 mm longus, orbicularis vel late obovatus, margine ⅔ proximalibus glandulis capitatis ornato, ⅓ distali glanduloso-fimbriato. Filamentum staminis postici erectum vel parum inclinatum versus petalum posticum. Glandulae staminodiorum subaequales. Stylus anticus 3.2–3.8 mm longus, arcuatus versus petalum posticum, styli postici 3.5–4.2 mm longi, semper anticum excedentes, divergentes, inclinati versus petala postico-lateralia; stigmata capitata. Ala dorsalis samarae 2.3–2.7 cm longa, 1.1–1.2 cm lata, alae laterales 3.2–4.5 mm latae, 9–10 mm altae.

Twining shrub. Vegetative branches purplish-brown, tomentulose and pubescent with T-shaped hairs or velutinous, pubescence abraded from older parts. Stem stipules 4.5–ca 9 mm long and wide, cordate, apex acute, finely, usually sparsely, velutinous-sericeous or glabrate adaxially, sericeous abaxially, deciduous; inflorescence stipules like the cauline, usually more densely pubescent, persistent or eventually deciduous. Stem leaves with the petiole 4.5–15 mm long, loosely but densely velutinous, laminas 3–10.2 cm long, 2.2–7.6 cm wide, narrowly to broadly elliptical, sometimes ovate or obovate, apex apiculate, base cordate, often the sinuses truncate, velutinous above, pubescent with T-shaped hairs or loosely tomentose below, a pair of sessile glands borne on the surface of the lamina 1.2–9.8 mm above the base, 2.3–6.5 mm from the costa, each gland 0.2–0.7 mm in diameter, sometimes one or both glands absent. Inflorescence leaves with the petiole at least ca 1.5 mm long, laminas abruptly smaller than the cauline or gradually decreasing in size toward the distal nodes, the smallest not less than 3.7 mm long, 1.1 mm wide, elliptical or lanceolate, velutinous above, sericeous or sericeous-tomentulose below, in the proximal leaves the pair of glands borne on the surface of the lamina, in the more distal at the base at the costa, each gland 0.2–0.7 mm in diameter. Inflorescence terminal or axillary, the axes velutinous or tomentulose-velutinous, internodes of the primary axis 1–4 (–6.7) cm long, 2° axes 1.7–7.3 cm long, subsidiary axes absent, at the more distal nodes the 2° axes suppressed, with 1 or 2 umbels borne on secondary peduncles in the leaf axil, always with 3 umbels at the terminal nodes, each umbel 4-flowered, primary peduncles absent, secondary peduncles up to 13 mm long. Bracts 0.4–1.9 mm long, 0.4–0.7 mm wide, narrowly to broadly triangular, glabrous, sometimes velutinous on the margins; bracteoles 0.3–0.7 mm long, 0.2–0.3 mm wide, oblong or triangular, glabrous, sometimes velutinous on the margins. Pedicels 18–25 mm long, velutinous or tomentulose-velutinous, equally long in fruit. Sepals 4.2–5 mm long, 1.8–2.5 mm wide, adaxially velutinous or tomentulose or velutinous-tomentulose, glands 1.6–2.5 mm long, 0.8–1 mm wide. Claw of the lateral petals 2–2.5 mm long, limb 11–12 mm long, 11–11.5 mm wide, orbicular, base attenuate, fimbriae up to 0.3 mm long, glandular. Claw of the posterior petal 4–4.5 mm long, limb 8.5–9 mm long and wide, orbicular or broadly obovate, fimbriae up to 0.3 (–0.4) mm long, those of the proximal ⅔ capitate-glandular, the distal ⅓ fimbriate-glandular. Filaments of the lateral stamens 3.8–4.4 mm long, posterior filament 3.2–3.7 mm long, erect or very slightly curved toward the posterior petal, anthers 1–1.2 mm long, glandular connective 0.6–0.7 mm long. Pollen grains 50–57 μm. Filament of the anterior staminode 3.7–3.9 mm long, anterior-lateral filaments 3.4–3.6 mm long, posterior-lateral filaments 3–3.2 mm long, inflexed between the posterior styles, all glands 1–1.1 mm long, ca 0.9 mm wide, sometimes the anterior gland a little larger than the lateral four, all glands with the apex and abaxial face smooth. Anterior style 3.2–3.8 mm long, ca 0.3 mm wide, always shorter and stouter than the posterior two, arced toward the posterior petal, posterior styles 3.5–4.2 mm long, ca 0.2 mm wide, divergent, inclined toward the posterior-lateral petals, all styles glabrous or with a few scattered hairs in the proximal ⅓ of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Carpophore up to ca 0.7 mm long. Torus up to ca 3.5 mm high. Samara with the dorsal wing 2.3–2.7 cm long, 1.1–1.2 cm wide, upper margin sigmoid, lower margin arced, straight or sigmoid, erose, lateral wings 3.2–4.5 mm wide, 9–10 mm high, rectangular, areole ca 3.5 mm long, ca 3 mm wide, nut ca 6 mm long, ca 3.6 mm in diameter, mature seeds not seen.

Type. *Smith & Reitz 12276.* Brazil. Santa Catarina: Ilha de Santa Catarina, Mun. Florianópolis, Canavieiras, 1–5 m, 28 Mar 1957 (holotype US, isotypes K, NY, P, R, RB).

Distribution. (Fig. 4). Known only from the beaches, dunes and adjacent areas along the coast of Santa Catarina and its islands.

BRAZIL. Santa Catarina: *Barclay 60* (MO, NY); Reserva Florestal dos Pilões, *Duarte 3339 & Falcão* (RB); Ilha de Santa Catarina, Morro das Pedras, 5 m, *Klein et al. 5834* (P); Ilha de Santa Catarina, Pantano do Sul, 2 m, *Klein & Bresolin 5988* (P); estrada a Itajaí, *Lutz s.n.* (R 129613); Morro da Santa Laguna, *Moreira & Moreira 495* (US); *Raben 443* (BR); Praia Braba, Itajaí, 1 m, *Reitz 3240* (US); Ilha de Santa Catarina, Campeche, *Reitz 5083* (US); Pilões, Palhoça, *Reitz & Klein 2752* (P); Rio dos Pinheiros, Braço do Norte, 100 m, *Reitz & Klein 6779* (P); Mun. Itajaí, Praia Braba, ca 26°58′S, 48°36′W, 3 m, *Smith & Reitz 6085* (R, RB); *Ule 711* (NY, fragment).

Peixotoa catarinensis is one of four species in which the terminal inflorescence nodes bear three umbels, i.e., are 12-flowered. The inflorescences are small compared to those of other species and rarely have more than two pairs of 2° axes. 3° axes have not been seen. *P. catarinensis* has unusually small leaf glands (0.2–0.7 mm in diameter), which are borne on the surface of the lamina away from the base and costa; sometimes they are absent. In some of the larger leaves the cordate base has truncate sinuses. *P. catarinensis* is the southernmost species in the genus and is known only from Santa Catarina. It is readily differentiated from the other three species with a similar but usually larger inflorescence. *P. parviflora*, which ranges from Minas Gerais to Paraná, and *P. tomentosa*, of Minas Gerais, have larger, basal leaf glands. In *P. adenopoda* of Bahia the leaf glands are borne on the lamina but are stalked and 0.8–1.5 mm in diameter. The range of the only other beach species, *P. hispidula*, extends from Bahia to São Paulo. It resembles *P. catarinensis* in its small inflorescences which bear petiolate leaves, but differs by its larger flowers and basal leaf glands.

Collected in flower throughout the year; only one fruiting collection (March).

8. Peixotoa cipoana C. Anderson, sp. nov. Fig. 18.

Frutex ascendens. Stipulae vegetativae 7–8.5 mm longae, persistentes. Petioli ca 1–5 mm longi. Laminae 3–9.5 cm longae, 2.7–6.7 cm latae, ovatae vel ellipticae interdum suborbiculares, rugosae, supra tomentulosae vel velutinae, subtus lanatae, basi juxta costam biglandulosae. Folia inflorescentiae subsessilia vel sessilia, distaliora linearia vel subulata. Inflorescentia terminalis, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 10–20 mm longi. Sepala 3.8–6 mm longa. Limbus petalorum lateralium 8.8–10.8 mm longus, orbicularis, margine glanduloso-fimbriato. Limbus petali postici 6–8 mm longus, ellipticus vel anguste obovatus, margine glandulis capitatis ornato. Glandula staminodii antici apice profunde indentata, indentatione in pagina abaxiali decurrenti; glandulae 4 staminodiorum lateralium apice non profunde indentatae. Stylus anticus 3.3–3.7 mm longus, erectus vel parum arcuatus versus petalum posticum, styli postici 3.4–4 mm longi, divergentes, parum inclinati versus petala postico-lateralia, semper anticum superantes; stigmata capitata. Samara ignota.

Scandent shrub. Vegetative branches velutinous-tomentulose. Stem stipules 7–8.5 mm long, (7.2–) 8–12 mm wide, broadly cordate, apex acute, glabrous or sometimes very sparsely velutinous or tomentulose adaxially, tomentulose-velutinous or woolly abaxially, persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 4.1 mm long, 4 mm wide, concave, more densely pubescent than the cauline, persistent or sometimes deciduous. Stem leaves with the petioles 1–5 mm long, densely tomentose-velutinous, laminas 3–9.5 cm long, 2.7–6.7 cm wide, ovate or elliptical, sometimes suborbicular, apex apiculate, base cordate, rugose, tomentulose or velutinous above, woolly below, a pair of sessile glands at the base at the costa, each gland 0.9–2.3 mm in diameter, sometimes with a second, smaller pair (0.6–1.2 mm in diameter) above, below or adjacent to the larger pair. Inflorescence leaves subsessile to sessile, laminas abruptly smaller than the cauline, the smallest

not less than 1.4 mm long, 0.4 mm wide, shape of the more proximal like the cauline, the more distal linear to subulate, apex acuminate, tomentose-velutinous or sparsely so above, woolly below, a pair of glands at the base at the costa, each gland 0.6–2 mm in diameter, sometimes with a second, smaller pair (0.2–0.9 mm in diameter) adjacent to the larger pair, one or both pairs sometimes fused, or sometimes a large gland on the costa with two large or small glands adjacent to it, or these three sometimes fused. Inflorescence terminal or axillary, the axes tomentulose-velutinous, internodes of the primary axis 1.7–8.2 cm long, 2° axes 1.5–13.6 cm long, 3° axes 1.2–2 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.8–2.2 mm long, 0.2–0.7 mm wide, narrowly triangular, glabrous adaxially, tomentulose-velutinous abaxially; bracteoles 0.1–0.4 mm long, 0.2–0.3 mm wide, linear, oblong, semicircular, or triangular, both surfaces glabrous or with a few scattered hairs, or sometimes tomentulose-velutinous abaxially and/or on the margins. Pedicels 10–20 mm long, tomentose. Sepals 3.8–6 mm long, 1.4–2.7 mm wide, adaxially the proximal ½–⅔ glabrous, the distal ⅓–½ tomentulose, glands (1.2–) 1.4–2.2 mm long, 0.7–1.1 mm wide. Claw of the lateral petals 2.3–3 mm long, limb 8.8–10.8 mm long, 8.5–11 mm wide, orbicular, base briefly attenuate, fimbriae up to 0.4 mm long, glandular. Claw of the posterior petal ca 3.7–4 mm long, limb 6–8 mm long, 4.8–6.2 mm wide, elliptical or narrowly obovate, fimbriae up to 0.2 (–0.4) mm long, capitate-glandular. Filaments of the lateral stamens 4–4.3 mm long, posterior filament 3–3.5 mm long, slightly curved toward the posterior petal, anthers 1.2–1.4 mm long, glandular connectives 0.8–1 mm long. Pollen grains 50–57 μm. Filament of the anterior staminode 4.1–4.5 mm long, anterior-lateral filaments 3.5–3.8 mm long, posterior-lateral filaments 3–3.5 mm long, slightly inflexed between the posterior styles, anterior and anterior-lateral glands 1.4–1.6 mm long, 1.3–1.5 mm wide, curved posterior-lateral glands 1.2–1.4 mm long, 1.1–1.3 mm wide, slightly curved, anterior gland with a deep indentation across the apex and decurrent on the abaxial face, the anterior-lateral and posterior-lateral glands with a shallower indentation. Anterior style 3.3–3.7 mm long, 0.3–0.4 mm wide, shorter than the posterior two, erect or very slightly inclined toward the posterior petal, posterior styles 3.4–4 mm long, divergent, slightly curved toward the posterior-lateral petals, all styles glabrous or more commonly with scattered hairs in the proximal ⅓ of their lengths, stigmas 0.3–0.5 mm in diameter, capitate. Samara not seen.

Type. *Occhioni 5009*. Brazil. Minas Gerais: Serra do Cipó, estrada da Conceição, 26 Jun 1973 (holotype RFA, isotype MICH).

Distribution. (Fig. 4). Known only from the Serra do Cipó of Minas Gerais.

BRAZIL. Minas Gerais: Serra do Cipó, estrada da Reprêsa, *Occhioni 5054* (MICH, RFA); Serra do Cipó, *Atala 62, 63* (R), *Damazio 2054* (RB), *Glassman & Gomes, Jr. 8064* (SP), *Vidal s.n.* (R 108249).

Peixotoa cipoana is unique in the genus in that its large staminode glands are recurved. All five glands have an indentation across the apex and decurrent on the abaxial face. In the posterior-lateral two the indentation is sometimes shallow. *P. cipoana* is also the only species in which the upper surface of the lamina of the stem leaves is sometimes tomentulose. The vesture is always velutinous in all the pubescent species except for *P. adenopoda* and *P. sericea*, in which it is sericeous. *P. cipoana* is readily separated from the other two species in the Serra do Espinhaço in which the leaves are densely tomentose or woolly below. *P. tomentosa* is recognized by its inflorescence in which the terminal nodes bear three umbels and thus are 12-flowered. Also, its staminode glands are straight and smooth. *P. spinensis* differs, in addition to its smaller, straight staminode glands, in its leaf glands which are borne on the surface of the lamina away from the margin and costa. The leaf glands of *P. cipoana* are basal.

Collected in flower in April, June, and July; two fruiting collections from April and July.

9. Peixotoa cordistipula Adr. Jussieu, Arch. Mus. Hist. Nat. Paris **3**: 431. 1843. Fig. 19.

Scandent shrub or subshrub or vine up to 1.5 m. Vegetative branches velutinous or velutinous-tomentose, pubescence sometimes abraded from older parts. Stem stipules 14–30 mm long, 10–20 mm wide, triangular or cordate-triangular, apex acute, notched or sometimes acuminate, velutinous adaxially, densely velutinous-tomentulose abaxially, deciduous; inflorescence stipules like the cauline or sometimes the most distal a little smaller, the smallest not less than 9 mm long, 7.5 mm wide, persistent. Stem leaves with the petiole 4.5–21 mm long, densely velutinous-tomentose, lamina 7–20.3 cm long, 3.5–14.5 cm wide, ovate or elliptical or sometimes orbicular, apex apiculate, base cordate or slightly so, velutinous above, tomentose below, usually densely so, with a pair of sessile glands at the base at the costa or sometimes halfway on the petiole, rarely up to 0.5 mm above the base at the costa, each gland 1–3.3 mm in diameter. Inflorescence leaves with the petiole (0.6–) 1 mm or more long, laminas abruptly smaller than the cauline, the smallest not less than (0.4–) 1.2 mm long, (0.2–) 1 mm wide, shape of the more proximal like the cauline, the more distal ovate or narrowly elliptical or lanceolate or linear, apex acuminate, sparsely velutinous or rarely glabrous above, densely velutinous below, with a pair of glands halfway on the petiole, each gland (0.4–) 0.7–2.1 mm in diameter, sometime with a second pair of smaller glands (0.4–1.4 mm in diameter) above or adjacent to the pair of larger glands. Inflorescence terminal or axillary, the axes densely velutinous, internodes of the primary axis 0.8–10 cm long, 2° axes 2–13 cm long, 3° axes 1–4.6 cm long, 4° axes 1.7–3.2 cm long, 5° axes 0.9–1.6 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary peduncles absent, secondary peduncles rarely present, up to 1 mm long; pedicels commonly arranged around a large glandular mass up to 2.5 mm in diameter, often sparsely velutinous, or the glandular tissue absent. Bracts (0.2–) 0.4–2.3 mm long, 0.2–0.5 mm wide, triangular or linear, glabrous or tomentulose abaxially or on the margins; bracteoles 0.1–0.4 mm long, 0.1–0.4 mm wide, triangular, linear or subulate, glabrous. Pedicels 11–32 mm long, densely velutinous, usually a little longer in fruit. Sepals 5–7.1 mm long, 2–4 mm wide, adaxially velutinous or sometimes the proximal ⅓–½ glabrous, the distal ½–⅔ pubescent with T-shaped hairs, glands 1.5–2.5 mm long, 0.9–1.1 mm wide. Claw of the lateral petals 2.2–3 mm long, limb 13–16 mm long, 11–15 mm wide, orbicular, base briefly attenuate or almost truncate, fimbriae up to 0.5 (–0.7) mm long, glandular. Claw of the posterior petal 3.8–4.5 mm long, limb 9.5–11.5 mm long, 8–11.5 mm wide, obovate, base briefly attenuate, fimbriae up to 0.6 mm long, those of the proximal ½–⅔ capitate-glandular, the distal ⅓–½ fimbriate-glandular. Lateral stamen filaments 4–5.2 mm long, posterior filament 3.5–4.5 mm long, usually shorter than the lateral filaments, very slightly inclined toward the posterior petal, anthers 1.4–1.6 mm long, glandular connectives 0.8–1 mm long. Pollen grains 50–57 μm. Anterior staminode filament 4.5–5.3 mm long, exceeding the anterior-lateral two, anterior-lateral filaments 4.2–4.8 mm long, usually exceeding the posterior-lateral two, posterior-lateral filaments 3.7–4 (–4.5) mm long, slightly inflexed between the posterior styles, anterior and anterior-lateral glands (1.3–) 1.5–1.9 mm long, (1.2–) 1.5–1.8 mm wide, posterior-lateral glands 1.1–1.5 mm long, 1.2–1.3 mm wide, all glands with the apex and abaxial face smooth. Anterior style (4.4–) 5–5.3 mm long, 0.3–0.4 mm wide, always at least a little longer than the posterior two, slightly arced toward the posterior petal, posterior styles 4.2–5 mm long, 0.3–0.4 mm wide, divergent, slightly arced

toward the posterior-lateral petals, all styles with scattered hairs in the proximal ⅓–½ of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Carpophore up to 4 mm long. Torus up to 7 mm high. Samara with the dorsal wing 2.3–3.4 cm long, 1.6–1.9 cm wide, upper margin arced, lower margin slightly arced or sigmoid, slightly erose, lateral wings 4.5–5.5 mm wide, 9–10 mm high, rectangular, areole 3.5–5 mm long, 4–7 mm wide, nut ca 5.8–ca 6.5 mm long, ca 3–5.5 mm in diameter, mature seeds not seen.

Type. *Martius 656*. Brazil. Mato Grosso: "In morro do Ernesto prope Cujaba [Cuiabá] . . ." (holotype P!, isotypes BM! BR! F! G! GH! K! LE! M! MO! NY! S! W!).

Distribution. (Fig. 5). Central Mato Grosso and eastern Bolivia; cerrado, dry woodlands, and at forest margins.

BOLIVIA. Chiquitos, *D'Orbigny 729* (P). BRAZIL. Mato Grosso: Mun. Rondonópolis, Serra da Petroliva, *Hatschbach 34713* (MBM, MICH); Cáceres, Giran, *Hoehne 158* (R); *Houllet* cat. no. 1051 (P); Serra Azul, ca 85 km S of Xavantina, 550 m, *Irwin et al. 17176* (MICH, NY, UB); Villa Maria, *Kuntze s.n.* (NY); inter Cuyaba [Cuiabá] et Diamantino, *Lindman A3533* (A, F, G, S); Cuyaba [Cuiabá], *Malme 1610, 1919* (S); Santa Ana da Chapada, *Malme s.n.* (S); ca 11 km W of KM 90, Xavantina-Aragarças Road, Vale dos Sonhos, 700 m, *Philcox & Freeman 4696* (K, NY, UB); vicinity of Buriti, Chapada dos Guimarães, 720 m, *Prance et al. 19239* (MICH); Serra da Chapada et Cuyaba [Cuiabá], *Riedel 1013* (LE, S); Santa Ana da Chapada, *Robert 347b* (K); between São Luiz Cáceres and Mato Grosso, *Sandeman 2134* (K, NY); Rio Juruena, Aripuanã, *Silva 3193* (MO, NY); Cuyaba [Cuiabá], *da Silva Manso (Lhotzky 99)* (G, W, syntype of *P. macrophylla*); Morro do Ernesto, Cuyaba [Cuiabá], *da Silva Manso* (*Lhotzky 117*) (BR); Santa Ana da Chapada, *Sladen 347* (BM); *H. Smith s.n.* (R 19721); *Veloso 1235, 1311*, (RB).

The dense, white pubescence of the vegetative parts of *P. cordistipula* gives the plants a silvery-grey appearance. The stem stipules are 14–30 mm long and 10–20 mm wide, and persist even after the inflorescence leaves and pedicels are shed. In umbels of *P. cordistipula* the pedicels are often arranged around a central, glandular mass, up to 2.5 mm in diameter. The only other species with

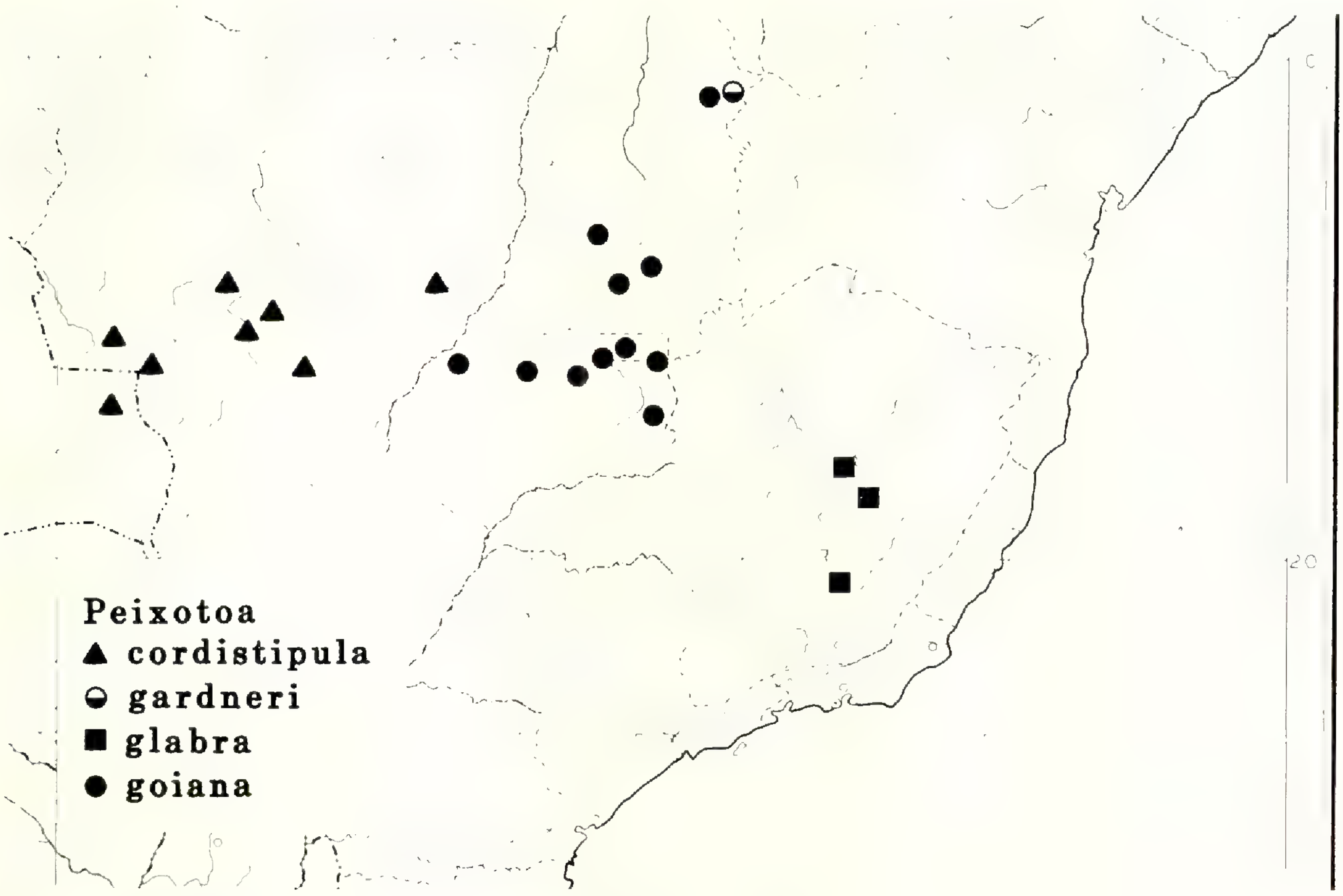

FIG. 5. Distribution of *P. cordistipula*, *P. gardneri*, *P. glabra*, and *P. goiana*.

such glandular tissue is *P. gardneri*, of northwestern Goiás, which has smaller, deciduous stipules. The western part of the range of *P. magnifica* overlaps with the range of *P. cordistipula*. Both species have petiolate inflorescence leaves, and large flowers and fruits. They are readily separated by their styles. Those of *P. magnifica* are 7–9.2 mm long. The anterior one is strongly arced toward the posterior petal and bears an oblong stigma at the apex but laterally on the abaxial surface. The styles of *P. cordistipula* are all less than 5.5 mm long and all stigmas are capitate. Both species produce large inflorescences, but in *P. magnifica* the flowers all open about the same time, while in *P. cordistipula* only a few are open at any one time.

Collections of *P. reticulata* with large stipules and/or from the western part of Brazil, from Bolivia, and from Paraguay have often been assigned to *P. cordistipula*. All the ones seen are apomicts with closed anthers that contain mostly aborted pollen. These plants have smaller and deciduous stipules and shorter staminode filaments than *P. cordistipula*. They lack the central, glandular mass in the umbel.

Collected in flower from April through August, in fruit in June and July.

10. Peixotoa gardneri C. Anderson, sp. nov. Fig. 13.

Frutex (?). Rami juniores dense aureo-velutini, vetustiores glabri; pili pes ca 0.5–1 mm longus. Stipulae vegetativae 7.5–10 mm longae, acutae vel bifidae, deciduae vel persistentes. Petioli 3–7 mm longi. Laminae 7.8–11.5 cm longae, 3.7–7 cm latae, ovatae vel anguste ellipticae vel lanceolatae, supra aureo-velutinae, subtus aureo-velutinae necnon ferentes pilos T-formes in venis, basi juxta costam biglandulosae vel interdum glandulis in lamina prope basim. Inflorescentia terminalis, ramis dense aureo-velutinis, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 16–24 mm longi. Sepala 5–7 mm longa. Limbus petalorum lateralium 11–11.5 mm longus, orbicularis, margine glanduloso-fimbriato. Limbus petali postici ca 8.5 mm longus, orbicularis, margine ⅔ proximalibus glandulis capitatis ornato ⅓ distali glanduloso-fimbriato vel glanduloso-denticulato. Stylus anticus 3.2–3.7 mm longus, posticis semper brevior, erectus, styli postici 3.5–4.2 mm longi, inaequales, erecti vel parum divergentes et inclinati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Shrub? Vegetative branches densely golden velutinous, stalks of the hairs usually 0.5–1 mm or more long, pubescence abraded from older parts. Stem stipules 7.5–10 mm long, 6.7–7.5 mm wide, cordate, entire with the apex notched, or bifid, glabrous adaxially, densely golden velutinous abaxially, deciduous or persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 5.5 mm long, 5.2 mm wide, apex of the more proximal notched, of the more distal acute, adaxially finely tomentulose, densely so in the proximal ¼–⅓, sometimes the distal ⅔–¾ glabrous or glabrate, abaxially densely golden tomentose or woolly, deciduous. Stem leaves with the petiole 3–7 mm long, densely golden velutinous, laminas 7.8–11.5 cm long, 3.7–7 cm wide, ovate or narrowly so or narrowly elliptical or lanceolate, apex apiculate, base cordate, golden velutinous above, golden velutinous and pubescent with T-shaped hairs on the veins below, a pair of sessile glands at the base at the costa or sometimes on the surface of the lamina up to 2 mm above the base, up to 0.5 mm from the costa. Inflorescence leaves of the proximal nodes petiolate, the more distal sessile, laminas abruptly smaller than the cauline, the smallest not less than 3.2 mm long, 0.6 mm wide, shape of the more proximal lanceolate or linear-lanceolate, of the more distal linear or subulate, apex acuminate, tomentose or sparsely tomentulose or glabrous above, densely golden velutinous-tomentose below, a pair of glands at the base of the

costa, each gland 0.7–2 mm in diameter, sometimes each gland with 1 or 2 smaller glands (0.4–0.5 mm in diameter) above and/or adjacent to it. Inflorescence terminal, the axes golden velutinous or velutinous-tomentulose, internodes of the primary axis (0.7–) 2–9 cm long, 2° axes 0.2–8.7 cm long, 3° axes 0.6–1.5 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent; the pedicels sometimes arranged around a glandular mass up to 0.8 mm in diameter, glabrous or sparsely to densely velutinous. Bracts 0.5–1.5 mm long, 0.3–0.7 mm wide, oblong, triangular or semicircular, glabrous adaxially, glabrous or velutinous or tomentose abaxially and/or on the margins; bracteoles 0.2–0.4 mm long, 0.2–0.3 mm wide, triangular, glabrous adaxially, glabrous or velutinous or tomentose abaxially and/or on the margins. Pedicels 16–24 mm long, velutinous or velutinous-tomentose, pubescence often dense. Sepals 5–7 mm long, 2.6–3.4 mm wide, adaxially densely tomentulose or glabrous in the proximal ⅓, the distal ⅔ densely tomentulose, glands 1.5–1.8 mm long, 1–1.3 mm wide. Claw of the lateral petals 2.2–2.5 mm long, limb 11–11.5 mm long, ca 12 mm wide, orbicular, base briefly attenuate, fimbriae up to 0.5 mm long, glandular. Claw of the posterior petal 4.2–5 mm long, limb ca 8.5 mm long, ca 9 mm wide, orbicular, fimbriate or denticulate, the fimbriae or teeth up to 0.3 mm long, those of the proximal ⅔ capitate-glandular, those of the distal ⅓ denticulate- or fimbriate-glandular. Filaments of the lateral stamens 4.2–4.3 mm long, posterior filament ca 3.6 mm long, erect or very slightly inclined toward the posterior petal, anthers 1.3–1.4 mm long, glandular connectives 0.7–0.8 mm long. Pollen grains 50–57 μm. Filaments of the anterior and anterior-lateral staminodes 3.6–3.8 mm long, posterior-lateral filaments ca 2.5 mm long, curved toward the posterior styles but not inflexed, all glands 1.6–1.7 mm long, anterior gland ca 1.5 mm wide, anterior-lateral and posterior-lateral glands 1–1.1 mm wide, all glands with the apex and abaxial face smooth. Anterior style 3.2–3.7 mm long, ca 0.4 mm wide, shorter than the posterior two, erect, posterior styles 3.5–4.2 mm long, unequal, erect or very slightly divergent and inclined toward the posterior-lateral petals, all styles glabrous, stigmas 0.4–0.5 mm wide, capitate. Samara not seen.

Type. *Gardner 3069 p.p.* Brazil. Goiás: Serra da Mangabeira [Chapada das Mangabeiras], Sep 1839 (holotype K, isotype K).

Peixotoa gardneri is known only from the type (Fig. 5). It resembles *P. anadenanthera* and especially *P. hirta* in that the hairs of the younger branches have very long stalks which are at last 0.5 mm long, but commonly are 1 mm or more. *P. anadenanthera* is easily recognized, since it is the only species in which the anthers lack the glandular connectives. *P. hirta* differs from *P. gardneri* in its smaller flowers. The limb of the posterior petal is obovate. In *P. gardneri* the limbs of all petals are orbicular. The pedicels of *P. gardneri* are sometimes arranged around a central, glandular mass which is often hidden in the dense pubescence. *P. cordistipula* of Mato Grosso is the only other species in which such glandular tissue is found in the umbel. The staminode glands of *P. gardneri* are unusual in that the adaxial groove extends nearly to the apex. However, this has been observed only in the two individuals of the type collection and may not be typical of the species. Extremely long adaxial grooves occur occasionally also in individuals of other species.
species.

Gardner 3069 is a mixed gathering. The two specimens deposited at K are *P. gardneri*. The specimen at BM is *P. goiana*.

This species is named for the intrepid George Gardner, one of the important early collectors of the Brazilian flora. He ventured into many remote areas, such as the Chapada das Mangabeiras where *P. gardneri* was collected, which have not been visited by botanists since his time.

11. Peixotoa glabra Adr. Jussieu in St. Hilaire, Fl. Bras. Mer. **3**: 60. t. 172. 1832 [1833]. Fig. 17.

Erect or procumbent, often virgate shrub up to 2 m. Vegetative branches shiny, purplish-brown, very sparsely velutinous when young, soon glabrous. Stem stipules 8–20 mm long, 7–10 mm wide, cordate or narrowly triangular, bifid or sometimes entire and the apex acute, glabrous adaxially, glabrous or sometimes sparsely velutinous abaxially, persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 5 mm long and wide, apex of the most distal acute or notched, commonly persistent. Stem leaves with the petiole 1.5–8.5 mm long, glabrous, lamina 5–12.2 cm long, 2.6–7.5 cm wide, elliptical, narrowly ovate or lanceolate, apex apiculate or acuminate, base cordate, glabrous above and below or rarely with a few scattered hairs along the margins, costa and major veins, a pair of sessile glands at the base at the costa or sometimes halfway on the petiole or rarely on the surface of the lamina up to 1.5 mm above the base, up to 1 mm from the costa, each gland 0.8–2.4 mm in diameter, sometimes one or both glands absent. Inflorescence leaves often petiolate at the most proximal nodes, subsessile or sessile at the most distal nodes, laminas gradually decreasing in size toward the distal nodes, the smallest not less than 1.7 mm long, 0.3 mm wide, lanceolate or triangular or linear or subulate, acuminate or rarely caudate, glabrous above and below or sometimes very sparsely velutinous, a pair of glands at the base, each gland 0.5–1.5 mm in diameter, these sometimes fused, or with 3–4 separate or fused glands, or with a second pair of smaller glands (0.5–0.7 mm in diameter) borne above the pair of larger glands. Inflorescence terminal, the axes glabrous or with a few scattered hairs or sometimes sparsely velutinous, internodes of the primary axis 2.7–10.7 cm long, 2° axes 1.7–9 cm long, 3° axes 0.8–5.9 cm long, 4° axes 1.6–2.6 cm long, 5° axes 0.7–0.9 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.7–1.6 mm long, 0.4–0.9 mm wide, narrowly triangular, apex obtuse, glabrous or with scattered hairs distally and/or on the margins; bracteoles 0.1–0.3 (–0.6) mm long, 0.2–0.4 mm wide, triangular, apex obtuse, glabrous. Pedicels 11–25 mm long, velutinous, sometimes a little longer in fruit. Sepals (3–) 3.8–6 mm long, (1.3–) 2–2.7 mm wide, adaxially the proximal ⅓ glabrous, the distal ⅔ tomentulose, glands 1.1–1.9 (–2.7) mm long, 0.8–1.9 mm wide. Claw of the lateral petals (1–) 1.3–3.3 mm long, limb (7.5–) 9.3–14 mm long, (7.4–) 8–14 mm wide, orbicular, base truncate or attenuate, fimbriae up to 0.5 mm long, glandular or eglandular. Claw of the posterior petal (2.5–) 3.3–4.6 mm long, limb (4–) 5.6–7.5 mm long, (3.2–) 3.8–4.5 mm wide, elliptical or oblong or slightly obovate, base truncate, all fimbriae up to 0.5 mm long and capitate-glandular, or those of the distal ¼ up to 0.7 mm long and fimbriate-glandular. Lateral stamen filaments (2.8–) 3–5 mm long, posterior filament 2.5–4 mm long, usually shorter than the lateral four, slightly arced toward the posterior petal, anthers 1–1.4 (1.6) mm long, glandular connectives 0.5–0.9 mm long. Pollen grains 50–54 μm. Anterior and anterior-lateral staminode filaments (3–) 3.5–4.7 mm long, posterior-lateral filaments 3–3.9 mm long, usually shorter than the anterior three, slightly inflexed between the posterior styles, glands 1.1–1.5 mm long, 1–1.5 mm wide, the anterior gland often a little larger than the other four, the anterior and anterior-lateral glands with a deep indentation across the apex and decurrent on the abaxial face, posterior-lateral glands smooth. Anterior style 3–4 mm long, 0.2–0.3 mm wide, gently arced toward the posterior petal, posterior styles 3.4–4.5 mm long, 0.2–0.3 mm wide, divergent, especially the distal ½ arced toward the posterior-lateral petals, all styles glabrous or sometimes with scattered hairs in the proximal ⅓ of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Carpophore up to 3.7 mm long. Torus up to 4.5 mm high.

Samara with the dorsal wing 1.6–2.7 cm long, 0.9–1.6 cm wide, upper margin gently sigmoid, lower margin straight, sometimes slightly erose, lateral wings 1.5–4 mm wide, 7–12 mm high, areole 3.5–5.5 mm long, 2.7–5.6 mm wide, nut 5.7–6.5 mm high, 4.2–6 mm in diameter, seed 5.7–6.1 mm long, outer cotyledon 7.6–7.9 mm long, 2.6–3 mm wide, folded at ca ½ of its length, inner cotyledon 4.8–5.1 mm long, 1.9–2.2 mm wide, folded at ca ⅔–¾ of its length.

Type. *St. Hilaire s.n.* Brazil. Minas Gerais: "in pascuis juxta Tijuco [Diamantina]" (holotype P!, isotype P!)

Distribution. (Fig. 5). Known only from the central part of the Serra do Espinhaço of Minas Gerais, especially from the environs of Diamantina; cerrado.

BRAZIL. Minas Gerais: ca 18 km SW of Diamantina on road to Curvelo, 1400 m, *Anderson 8511* (MICH, NY); Mun. Gouvêia, 35 km SW of Diamantina on BR-259, 1250 m, *Anderson 11549* (C, MICH); ca 10 km SW of Diamantina, *Anderson et al. 35189* (MO, NY); Diamantina, *Brade 13722, 13775, 13777, 13781* (RB); Serra dos Cristais, Diamantina, *Glaziou 18937* (C, K, NY, P); Mun. Sêrro, rod. MG-2, entre Sêrro e Datas, *Hatschbach 28921* (NY, P); ca 20 km S of São João da Chapada, 1200 m, *Irwin et al. 28371* (MICH, MO, NY); ca 10 km S of São João da Chapada, 1200 m, *Irwin et al. 28412* (MICH, MO, NY); Serra da Lapa, *Langsdorff s.n.* (LE); Serra do São Gonçalo prope Diamantina, *do Linea* (*Herb. Schwacke 12816*) (RB); just W of Sêrro, on road from Conceição to Diamantina, *Maguire 49144* (MICH, NY); between Diamantina and Gouvêia, *Maguire 49164* (NY); Serra Frio, ad Tejuco [Diamantina], *Martius 1343* (M); Ouro Preto, Villa Rica [Ouro Preto], *Martius s.n.* (two collections) (M); Diamantina, crest of Serra do Rio Grande, 1300 m, *Mexia 5804* (A, BM, F, G, GH, K, MICH, MO, NY, R, S, US); Diamantina, *Pereira 1535* (RB); *Riedel XII p.p.* (LE, S); Serra da Lapa, *Riedel 1156* (LE, S); ad Riacho das Varas prope Diamantina, *Schwacke 8370* (RB); Tejuco [Diamantina], *Vauthier 459* (G, GH, P); Morro dos Cruzeiros, Diamantina, ca 1300 m, *Vidal s.n.* (R 72121).

Peixotoa glabra is the only glabrous species in Minas Gerais. The very sparsely pubescent *P. irwinii* and some glabrous forms of *P. reticulata* occur in the same area, but are readily distinguished by the staminode glands. Those of *P. glabra* are of equal size. The anterior and anterior-lateral three have an indentation across the apex and decurrent on the abaxial face. The glands of *P. irwinii* are smaller, unequal, and have a smooth apex. The abaxial face of the anterior and anterior-lateral glands have a shallow, broad depression. Also, the petioles of *P. irwinii* are golden pubescent. Those of *P. glabra* are glabrous. In *P. reticulata* the staminode glands are smooth and usually unequal. Its flowers are usually larger than those of *P. glabra*. *Anderson 8564* is perhaps a hybrid between *P. glabra* and *P. reticulata*. The specimens look like *P. reticulata*, but the foliage and stems are glabrous and the staminode glands are indented. The flowers, as in nearly all collections of *P. reticulata*, have closed anthers containing aborted pollen.

Peixotoa glabra has sometimes been confused with the usually glabrous or glabrate *P. hispidula*, which grows along the coast from Bahia to São Paulo. It differs in its usually large flowers born in a single umbel or a small inflorescence. The staminode glands are strongly dimorphic. The inflorescence leaves are all petiolate. Those of *P. glabra* are sessile at the more distal nodes.

Though *P. glabra* is apparently another narrow endemic, it is well represented in herbaria. Diamantina was an important destination for early collectors and still is much visited today. The locality of two Martius collections in the Munich herbarium is given as Ouro Preto, another frequently collected area. While it is tempting to ascribe this to a mistake in labeling, it must be remembered that the flora of Minas Gerais is still only poorly known.

Collected in flower from December through August, in fruit from March through August.

12. Peixotoa goiana C. Anderson, sp. nov. Figs. 2, 20.

Suffrutex, caules ascendentes usque ad 2 m. Stipulae vegetativae 4–19 mm longae, acutae vel bifidae, plerumque persistentes. Petioli 1–7(–9) mm longi.

Laminae (4.3–)5–17 cm longae, 2.3–10.6 cm latae, lanceolatae vel ellipticae vel ovatae vel suborbiculares, supra velutinae raro glabrae, subtus ferentes pilos T-formes vel non nisi in venis vel raro glabrae, basi juxta costam biglandulosae vel interdum glandulis in lamina prope basim. Folia inflorescentiae petiolo brevi vel sessilia, in nodis distalibus linearia vel subulata. Inflorescentia terminalis, umbellis singularibus. Bracteae bracteolaeque plerumque praesentes interdum absentes. Pedicelli 10–34 mm longi. Sepala 4–6.5 mm longa. Limbus petalorum lateralium 9.6–12(–15) mm longus, orbicularis vel late ellipticus, margine glanduloso-denticulato vel glanduloso-fimbriato interdum eglanduloso. Limbus petali postici 7.5–8.3(–10) mm longus, orbicularis vel interdum late obovatus, margine glandulis capitatis ornato vel margine ⅔ proximalibus glandulis capitatis ornato ⅓ distali glanduloso-fimbriato vel glanduloso-denticulato. Glandulae 3 staminodiorum anticorum plerumque apice profunde indentatae, indentatione in pagina abaxiali decurrenti, interdum laeves. Stylus anticus (2.6–)3.1–4.3(–4.6) mm longus, plerumque erectus raro parum inclinatus versus petalum posticum, styli postici 3.3–4.7 mm longi, divergentes, plerumque saltem parum inclinati versus petala postico-lateralia, semper anticum superantes; stigmata capitata. Ala dorsalis samarae 1.6–2.7 cm longa, 1.1–1.9 cm lata, alae laterales 0.6–2.5 mm latae, 5.5–9.8 mm altae, erosae interdum dissectae.

Subshrub with one or few ascending stems to 2 m. Vegetative branches densely, usually golden, velutinous or tomentulose-velutinous, rarely glabrous; the pubescence often abraded from older parts. Stem stipules 4–19 mm long, 2.3–16.5 mm wide, cordate or triangular-cordate, sometimes narrowly so, entire with the apex acute or notched, or bifid, finely velutinous or sparsely so or glabrous adaxially, densely velutinous or densely or sparsely tomentose or tomentose-velutinous abaxially, usually persistent; inflorescence stipules of the proximal nodes equal or larger than the cauline, the distal gradually decreasing in size toward the distal nodes, the smallest not less than 5.8 mm long, 5.3 mm wide, cordate, often concave, entire with the apex acute, the most proximal sometimes with the apex notched, or bifid, velutinous or sparsely so adaxially, velutinous-tomentulose abaxially, usually deciduous. Stem leaves with the petiole 1–7 (–9) mm long, densely, usually golden velutinous or rarely glabrous, laminas (4.3–) 5–17 cm long, 2.3–10.6 cm wide, lanceolate or elliptical or narrowly so or ovate or suborbicular, apex apiculate, base cordate, rugose, velutinous or rarely glabrous above, sparsely to densely pubescent with T-shaped hairs or rarely tomentose or rarely the hairs restricted to the veins or rarely glabrous below, hairs usually golden above and below, a pair of sessile glands halfway on the petiole or sometimes at the base at the costa, sometimes borne on the surface of the lamina 1–6 mm above the base, up to 3.8 mm from the costa, rarely at the margin 0.7–1 mm from the costa, each gland 0.5–1.8 mm in diameter, sometimes with a second, smaller pair (0.4–0.5 mm in diameter) below or adjacent to the larger pair. Inflorescence leaves of the proximal nodes with the petiole up to 5 (–6) mm long, the more distal sessile or very rarely with a petiole up to 1.4 mm long, laminas abruptly smaller than the cauline or gradually decreasing toward the distal nodes, the smallest not less than 2 mm long, 0.2 mm wide, the more proximal elliptical or narrowly so, the more distal linear, or subulate, apex acuminate, vesture of the more proximal like the cauline, the more distal glabrous above, densely velutinous below, all with a pair of glands at the base at the costa, the glands rarely fused, each gland (0.2–) 0.5–1.8 mm in diameter, sometimes with a second, smaller pair (0.3–1.2 mm in diameter) above or adjacent to the larger pair, or rarely one large gland borne on the costa with two large glands on either side. Inflorescence terminal, the axes velutinous or tomentulose, usually densely, rarely sparsely so, internodes of the primary axes 3.2–18.4 cm long, 2° axes 1.3–16.5 cm long, 2° subsidiary axes (0.2–) 1.5–3.5 cm long, 3° axes 0.6–7.2 cm long, 4° axes 1–3.8 cm long, 5° axes 0.9–1.8 cm long;

umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.3–1.3 mm long, 0.3–1.2 mm wide, triangular or semicircular, glabrous, sometimes velutinous or sparsely so abaxially and/or on the margins; bracteoles 0.1–0.5 mm long, 0.2–0.4 mm wide, triangular, glabrous, rarely velutinous abaxially and/or on the margins; bracts and bracteoles sometimes absent. Pedicels 10–34 mm long, (usually golden) densely velutinous or tomentose, becoming up to ⅓ again as long in fruit. Sepals 4–6.5 mm long, 2.2–3.3 mm wide, adaxially the proximal ¼–⅔ velutinous or sparsely so, the distal ¾–⅓ tomentulose, sometimes entirely sparsely velutinous, glands 1.6–2.6 mm long, 0.6–1.2 mm wide. Claw of the lateral petals 2.2–3.2 mm long, limb 9.6–12 (–15) mm long, 9–12 (–15) mm wide, orbicular or rarely broadly elliptical, base briefly attenuate, denticulate or fimbriate or both, the teeth and fimbriae up to 0.5 (–0.8) mm long, glandular or eglandular. Claw of the posterior petal 4–5 mm long, limb 7.5–8.3 (–10) mm long, 6.8–8 (–9) mm wide, orbicular or rarely broadly obovate, denticulate or fimbriate, teeth and fimbriae up to 0.6 mm long, those of the proximal ½–⅔ capitate-glandular, the distal ½–⅓ denticulate- or fimbriate-glandular, or sometimes all capitate-glandular. Filaments of the lateral stamens (3.3–) 3.8–4.8 mm long, posterior filament 2.6–4.3 mm long, always shorter than the lateral four, erect or very slightly curved toward the posterior petal, anthers 1.5–1.7 mm long, glandular connectives 0.7–0.8 mm long. Pollen grains ca 57 μm. Filament of the anterior staminode 3.5–4.4 mm long, usually exceeding the anterior-lateral two, anterior-lateral filaments 3.2–3.6 mm long, posterior-lateral filaments 2.8–3.5 mm long, always shorter than the anterior-lateral two, inflexed between the posterior styles, anterior gland 1.2–1.5 mm long, 1.2–1.3 mm wide, anterior-lateral glands ca 1.2 mm long, 1.1–1.2 mm wide, posterior-lateral glands 1–1.1 mm long, 0.9–1 mm wide, anterior and anterior-lateral glands with a deep indentation across the apex and decurrent on the abaxial face or sometimes smooth, posterior-lateral glands smooth. Anterior style (2.6–) 3.1–4.3 (–4.6) mm long, 0.3–0.4 mm wide, erect or rarely slightly inclined toward the posterior petal, posterior styles 3.3–4.7 mm long, ca 0.3 mm wide, always longer than the anterior style, divergent, at least slightly inclined toward the posterior-lateral petals, all styles glabrous or with scattered hairs in the proximal ½ of their lengths, stigmas 0.3–0.5 mm wide, capitate. Carpophore up to 3.6 mm long. Torus up to 6.2 mm high. Samara with the dorsal wing 1.6–2.7 cm long, 1.1–1.9 cm wide, upper margin sigmoid or arced, lower margin sigmoid, arced or semicircular, slightly erose, lateral wings 0.6–2.5 mm wide, 5.5–9.8 mm high, rectangular, erose or irregularly dentate or dissected, areole 4.5–6.1 mm long, 3.5–5.5 mm wide, nut 5.5–7 mm long, 3–5 mm in diameter, seed 6.9–8.2 mm long, outer cotyledon 7.8–10.8 mm long, 1.6–3.3 mm wide, folded at ca ⅔ of its length, inner cotyledon 5.1–7.2 mm long, 1.5–2 mm wide, folded at ca 2/3–6/7 of its length or straight.

Type. *Irwin et al. 12855*. Brazil. Goiás: Chapada dos Veadeiros, 14°S, 47°W, ca 15 km W of Veadeiros [Alto Paraíso], 1000 m, 14 Feb 1966 (holotype UB, isotypes MICH, NY).

Distribution. (Fig. 5). Central Goiás, especially in the Serra dos Veadeiros, Serra dos Cristais, Serra dos Pirineus, and Serra Dourada, and the Distrito Federal; cerrado and campo.

BRAZIL. Goiás: Chapada dos Veadeiros, ca 20 km N of Alto Paraíso, ca 1600 m, *Anderson 6201* (MICH, NY); Serra dos Cristais, 9 km S of Cristalina on road to Catalão, 1170 m, *Anderson 8090* (NY); Serra Dourada, ca 15 km (str. line) S of Goiás Velho, 1000 m, *Anderson 10024* (MICH, NY); Serra dos Pirineus, ca 15 km (str. line) N of Corumbá de Goiás, 1300 m, *Anderson 10282* (MICH, NY); Chapada dos Veadeiros, 14°S, 47°30′W, 2.5 km E of Alto Paraíso, *Estabrook 8* (MICH); Chapada dos Veadeiros, *Ferreira 6* (UB); Serra dos Pirineus, *Ferreira 8* (UB); Serra da Mangabeira [Chapada das Mangabeiras] *Gardner 3069 p.p.* (BM); Chapada dos Veadaeiros, Pouso Alto, 1800 m, *Ferreira 10, 11* (UB); Serra Dourada, *Ferreira 32* (UB); ca 70 km de Braslândia, Vale S. Gerônimo, *Ferreira 150, 152* (UB); Chapada dos Veadeiros, mun. Alto Paraíso, 16 km by road N of Alto Paraíso, 1600 m,

14°S, 47°W,*Gates & Estabrook 103* (MICH); Serra dos Pirineus, Pirenópolis, *Giulietti & Lima 725* (UB); Chapada dos Veadeiros, Pouso Alto, 1800 m, *Graziela [Barroso] 609* (UB); Chapada dos Veadeiros, 65 km N of Brasília, *Harley et al. 11432* (K, NY); Serra do Rio Preto, 16°S, 47°W, ca 5 km E of Goiás boundary on road to Guarapuá, M. G., 1000 m, *Irwin et al. 10291* (MICH); Serra dos Pirineus, 16°S, 49°W, ca 14 km S of Corumbá, 975 m, *Irwin et al. 10773* (NY); Serra Dourada, 20 km SE of Goiás Velho, 800 m, *Irwin et al.* 11705 (MICH, NY); Chapada dos Veadeiros, 14°S, 47°W, ca 15 km W of Veadeiros [Alto Paraíso], *Irwin et al. 12351* (MICH, NY); Serra dos Cristais, 17°, 48°W, ca 10 km S of Cristalina, 1200 m, *Irwin et al. 13733* (MICH, NY); ca 87 km SE of Aragarças, 700 m, *Irwin et al. 17562* (MICH); Serra dos Pirineus, 15–20 km N of Corumbá de Goiás on road to Niquelândia, ca 1150 m, *Irwin et al. 18616* (MICH, NY), *19271* (NY); Chapada dos Veadeiros, ca 10 km W of Alto Paraíso, 1000 m, *Irwin et al. 24985* (NY); Chapada dos Veadeiros, ca 19 km N of Alto Paraíso, ca 1250 m, *Irwin et al. 32799* (MICH, NY); Serra dos Pirineus, ca 18–20 km E of Pirenópolis, 1000 m, *Irwin et al. 34061* (MICH, NY), *34096* (NY); 14 km S of Niquelândia, ca 750 m, *Irwin et al. 34743, 34744* (NY); Niquelândia, *Macêdo 3671* (RB); Chapada dos Veadeiros, 2 km from Veadeiros [Alto Paraíso], *Prance & Silva 58200* (MICH, NY); Serra Dourada, *Rizzo 3997, 4128, 4442, 4494, 4597, 4638* (RB); mun. Alto Paraíso, Cinturão Verde, Parque Nacional do Tocantins, *Rosa 67* (UB). Distrito Federal: Brasília, *Andrade 318 & Emmerich 310* (R), *Ferreira 2a, 46, 47, 118* (UB), *Gomes 1056* (RB), *8394* (SP, UB), *Irwin & Soderstrom 6083a* (NY), *Martin 407* (GH), *476* (GH, UB), *Occhioni 23* (MICH), *Pires et al. 9086* (UB, US), *Sucre 274* (NY, RB, UB); Braslândia, *Ferreira 4* (UB); summit of Chapada da Contagem, ca 10 km E of Brasília, 1000 m, *Irwin et al. 8221* (MICH); ca 12 km W of Taguatinga on road to Braslândia, 1250 m, *Irwin et al. 10683* (NY); Braslândia, *Macêdo 23* (UB); Chapada da Contagem, along highway DF-5 about 36 km W of intersection with BR-020, 1280 m, *Plowman 9943* (MICH); Fazenda Agua Limpa (Univ. of Brasília field station), near Vargem Bonita, *Ratter et al. 2806, 2899, 3129* (MICH); Salinas, *Weddell 2193* (P).

Peixotoa goiana is distinguished by its flowers and inflorescence leaves. All the petals have an orbicular (rarely broadly obovate or broadly elliptical) limb. The margins of the lateral limbs are commonly denticulate or sometimes fimbriate. The anterior style is usually erect or sometimes slightly inclined toward the posterior petal. The anterior and anterior-lateral staminode glands of plants from the Distrito Federal, the Serra dos Pirineus and the Serra dos Cristais have an indentation across the apex and decurent on the abaxial face. Those of the Serra Dourada are smooth. In specimens from the Chapada dos Veadeiros the glands are either indented, often shallowly so, or smooth. The inflorescence leaves of the more distal nodes are linear to subulate and sessile; only *Irwin 17562* has inflorescence leaves with tiny petioles. This collection is from the extreme western part of the range at the Mato Grosso border.

The abundance of hairs on the vegetative parts is highly variable. Most plants are moderately to densely pubescent, but in some the hairs are very sparsely distributed and on the leaves restricted to the major veins. Glabrous forms are rare (*Anderson 8090, Irwin 10773, Macêdo 3671*). The stem and inflorescence stipules are usually 4–12 mm long. However, in a few collections their length ranges from 9–19 mm.

The samaras have relatively narrow lateral wings which are 0.6–2.5 mm wide. In most specimens the wings are at least 1 mm wide. Only the probably closely related *P. hatschbachii* has more reduced wings. In that species each lateral wing is a narrow strip less than 1 mm wide in the proximal ½ of the nut or a crest, or the lateral wings are absent. In *P. goiana* the wings extend along the entire length of the nut.

In the southern part of its range *P. goiana* overlaps with the apomictic *P. reticulata*. Some plants that are intermediate, especially in floral characters, occur, but all are apparently apomictic.

Collected in flower and fruit throughout the year.

13. Peixotoa hatschbachii C. Anderson, sp. nov. Fig. 15.

Frutex erectus usque ad 1.2 m. Caules glabri. Stipulae vegetativae 17–19.5 mm longae, plerumque bifidae, deciduae vel persistentes. Petioli 6.5–10 mm longi. Laminae 6.2–9.3 cm longae, 4.4–7.5 cm latae, ovatae, rugosae,

glabrae, basi juxta costam 2– vel 4–glandulosae, glandulis pedicellis. Folia inflorescentiae petiolo brevi vel sessilia, distaliora linearia vel subulata, subtus dense velutina, basi juxta costam 2–6–glandulosa. Inflorescentia terminalis (vel axillaris?), umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 18.3–23 mm longi. Sepala 4.5–5.2 mm longa. Limbus petalorum lateralium 9.8–10 mm longus, late obovatus vel suborbicularis, margine glanduloso-fimbriato. Limbus petali postici 3.5–3.8 mm longus, obovatus vel late obovatus, margine ½ proxmali glandulis capitatis ornato, ½ distali glanduloso-fimbriato. Styli subaequales, 3.6–4 mm longi, anticus parum inclinatus versus petalum posticum, postici divergentes, parum inclinati versus petala postico-lateralia; stigmata capitata. Ala dorsalis samarae 1.7–1.9 cm longa, 1.3–1.4 cm lata, alae laterales absentes vel multo redactae, minus quam 1.5 mm latae, 5.5–7.2 mm altae, extensae e medio nucis ad basim.

Erect shrub to 1.2 m. Vegetative branches shiny, purple, glabrous. Stem stipules 17–19.5 mm long, 18–19 mm wide, cordate, bifid, glabrous, persistent or deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 8.3 mm long, 10.5 mm wide, entire, apex acute, tomentulose adaxially, velutinous abaxially, deciduous. Stem leaves with the petiole 6.5–10 mm long, glabrous, laminas 6.2–9.3 cm long, 4.4–7.5 cm wide, ovate, apex apiculate, base cordate, rugose, glabrous above and below, a pair of stalked glands at or just above the base at the costa, each gland 1–1.2 mm in diameter, stalk 0.8–1.2 mm long, commonly each gland with an adjacent smaller gland, 0.8–1.1 mm in diameter, stalk 0.4–1 mm long. The more proximal inflorescence leaves with a petiole up to 5 mm long, the more distal commonly sessile, laminas abruptly smaller than the cauline, the smallest not less than 5.5 mm long, 0.6 mm wide, shape of the more proximal like the cauline, the more distal linear to subulate, apex acuminate, sparsely velutinous or glabrous above, densely velutinous below, glands sessile, sometimes with a pair of glands at the base at the costa, usually with multiple glands: one pair but each large gland with one or two smaller glands adjacent and/or below it, some or all of these sometimes fused, or sometimes with one large gland on the costa and two smaller glands adjacent on each side, or sometimes with two large glands at each side of the costa, some or all of these fused, and with one or two smaller glands below them, each large gland 1–1.5 mm in diameter, each small gland 0.5–1 mm in diameter. Inflorescence terminal (or axillary ?), the axes sparsely velutinous to glabrate, internodes of the primary axis 10–13 cm long, 2° axes 5.8–19 cm long, 2° subsidiary axes up to 2.7 cm long, 3° axes 3.8–7.1 cm long, 3° subsidiary axes 1.2–1.5 cm long, 4° axes 1.8–3.1 cm long, umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 1.8–4 mm long, 0.6–9 mm wide, narrowly triangular, glabrous adaxially, sparsely velutinous abaxially; bracteoles 0.2–0.3 mm long, 0.3–0.5 mm wide, semicircular, glabrous. Pedicels 18.3–23 mm long, velutinous, slightly longer in fruit. Sepals 4.5–5.2 mm long, 2.1–2.6 mm wide, adaxially the proximal ½–⅔ glabrous, the distal ½–⅓ tomentulose, glands 1.7–2 mm long, 0.6–1 mm wide. Claw of the lateral petals 2–2.2 mm long, limb 9.8–10 mm long, 9–10 mm wide, broadly obovate to suborbicular, base attenuate, fimbriae up to 0.6 mm long, glandular. Claw of the posterior petal 3.5–3.8 mm long, limb 5.5–6.5 mm long, 5–5.8 mm wide, obovate or broadly so, fimbriae up to 0.4 mm long, those of the proximal ½ capitate-glandular, the distal ½ fimbriate-glandular. Lateral stamen filaments 3.6–4 mm long, posterior filament (3–) 3.5–3.7 mm long, arced toward the posterior petal, anthers 1.5–1.8 mm long, glandular connectives 0.7–0.9 mm long. Pollen grains 50–57 μm. Anterior staminode filament 3.8–4 mm long, anterior-lateral filaments 3.6–3.7 mm long, posterior-lateral filaments 3.2–3.4 mm long, inflexed between the posterior styles, anterior and anterior-lateral glands 1.3–1.4 mm long, 1.1–1.2 mm wide, posterior-lateral glands ca 1.1 mm long, ca 0.8 mm wide,

all glands with the apex and abaxial face smooth. Styles 3.6–4 mm long, equal or the anterior style a little longer or shorter than the posterior two, anterior style ca 0.4 mm wide, slightly inclined toward the posterior petal, posterior styles ca 0.3 mm wide, divergent, slightly inclined toward the posterior-lateral petals, all with some scattered hairs in the proximal ¼ of their lengths, stigmas 0.5–0.6 mm in diameter, capitate. Carpophore up to 3 mm long. Torus up to ca 5 mm high. Samara with the dorsal wing 1.7–1.9 cm long, 1.3–1.4 cm wide, upper margin gently arced, lower margin slightly erose or sometimes entire, lateral wings absent or reduced to a crest or to a narrow, erose strip less than 1.5 mm wide, 5.5–7.2 mm high, usually extending from the middle to the base of the nut, areole 5–5.3 mm long, ca 5 mm wide, nut 6–7 mm long, 4.7–5 mm in diameter, seed ca 6.8 mm long, ca 3 mm wide, outer cotyledon ca 9.7 mm long, ca 2.8 mm wide, folded at ½ of its length, inner cotyledon ca 5.2 mm long, ca 1.6 mm wide, folded at ca 4/5 of its length.

Type. *Hatschbach 36675*. Brazil. Goiás: BR–135, 10 km E of Anápolis, 22 May 1975 (holotype MBM, isotypes C, MICH).

Peixotoa hatschbachii is known only from the type (Fig. 6). It is distinguished by its stalked leaf glands and by its glabrous vegetative branches and stem leaves. The samaras are unique in that the lateral wings are absent, or reduced to a crest or a narrow strip of tissue, less than 1.5 mm wide, which usually extends from the middle to the base of the nut. The stipules are unusually large. Those of the stem are 17–19.5 mm long and wide. The smallest inflorescence stipule seen is 8.3 mm long an 10.5 mm wide. *P. hatschbachii* occurs within the range of *P. goiana*, to which it may be closely related. Plants of *P. goiana* are only rarely glabrous. These glabrous forms as well as the glabrous or very sparsely pubescent *P. psilophylla* from east-central Mato Grosso differ from *P. hatschbachii* by their sessile leaf glands, smaller stipules, and larger posterior petals.

This species is named in honor of Gert Hatschbach, an astute student as well as a prolific and discerning collector of the flora of central and southern Brazil.

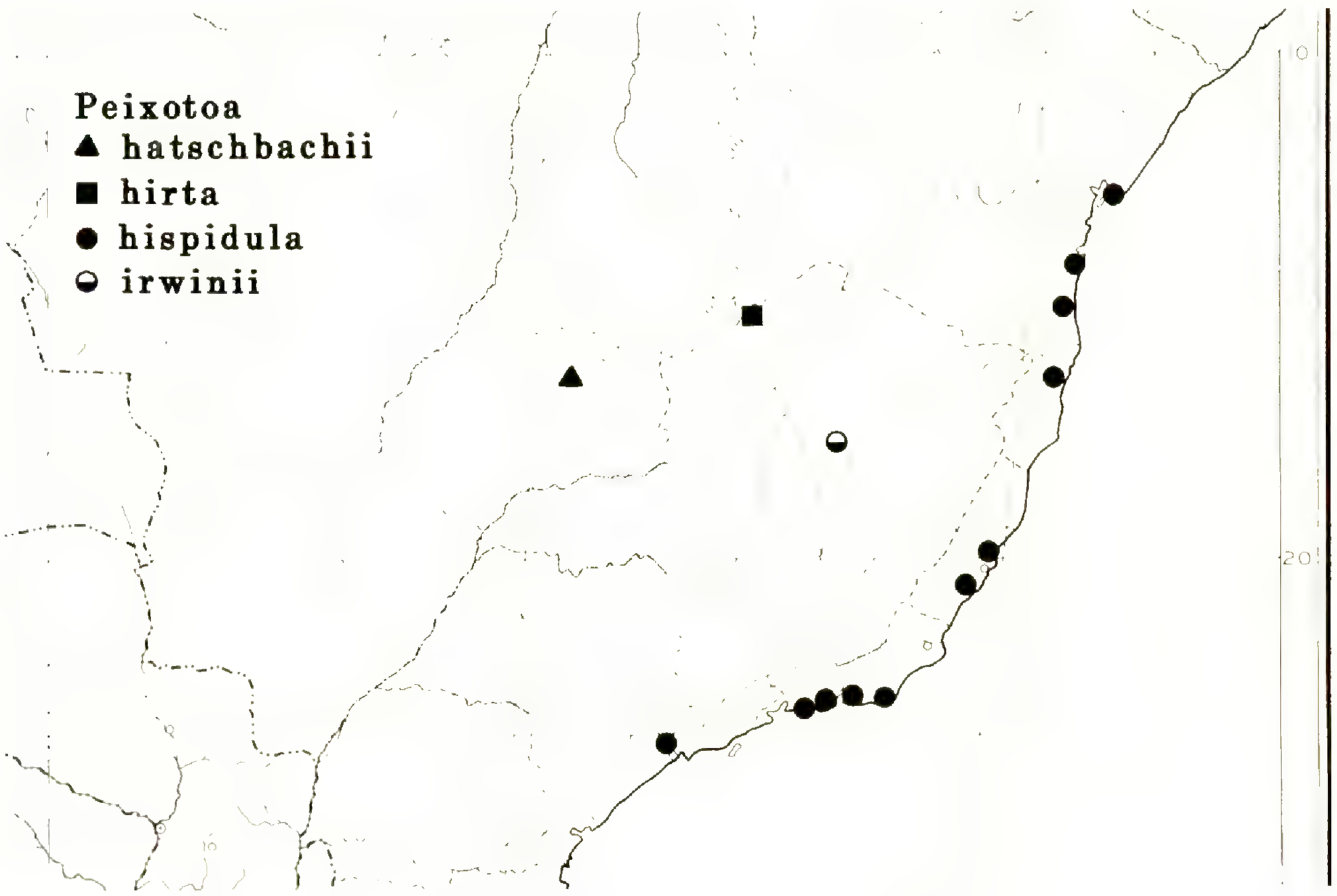

FIG. 6. Distribution of *P. hatschbachii, P. hirta, P. hispidula,* and *P. irwinii.*

14. Peixotoa hirta Adr. Jussieu, Ann. Sci. Nat. Sér. II, Bot. **3**: 279. 1840. Fig. 20.

Erect, subscandent shrub, 1–2 m. Vegetative branches densely but loosely golden velutinous, stalks of the hairs usually 0.5–1 mm or more long, pubescence abraded from older parts. Stem stipules 6–9 mm long, 7–9 mm wide, cordate, entire with the apex acute or notched, or bifid, glabrous or sparsely tomentulose adaxially, velutinous and pubescent with T-shaped hairs abaxially, deciduous; inflorescence stipules like the cauline or sometimes a little larger, glabrous adaxially, tomentose abaxially, deciduous. Stem leaves sessile or with the petiole up to 6.5 mm long, densely golden velutinous, laminas 7.3–9 cm long, 4.7–8.2 cm wide, elliptical or ovate or suborbicular, rugose, apex apiculate, base cordate, loosely golden velutinous and pubescent with golden T-shaped hairs above, densely pubescent with golden T-shaped hairs below, a pair of sessile glands at the base at the costa, each gland 0.6–1.2 mm in diameter. Inflorescence leaves with the petiole up to 3.2 mm long, the more distal sessile, laminas abruptly smaller than the cauline, the smallest not less than 3 mm long, 0.6 mm wide, narrowly lanceolate to subulate, apex acuminate, densely golden velutinous or tomentulose above, very densely pubescent with golden T-shaped hairs below, a pair of glands at the base at the costa, each gland 0.6–2.5 mm in diameter. Inflorescence terminal, the axes densely but loosely golden velutinous, internodes of the primary axis 4.5–10.7 cm long, 2° axes 0.7–4.7 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.9–1.2 mm long, 0.6–0.8 mm wide, triangular, glabrous; bracteoles ca 0.2 mm long and wide, oblong or triangular, glabrous. Pedicels 11–15 mm long, densely golden tomentose. Sepals 4.4–5.8 mm long, 2.1–3 mm wide, adaxially glabrous, glands 1.5–2 mm long, 0.6–1.1 mm wide. Claw of the lateral petals 2.2–2.4 mm long, limb 9–9.5 mm long, ca 8–8.5 mm wide, orbicular, base truncate, fimbriae up to 0.5 mm long, fimbriate-glandular, sometimes a few fimbriae of the anterior-lateral petals eglandular. Claw of the posterior petal 2.5–2.6 mm long, limb ca 6.5 mm long, ca 5 mm wide, obovate, fimbriae up to 0.6 mm long, capitate-glandular. Lateral stamen filaments 3.3–3.4 mm long, posterior filament ca 3.2 mm long, erect or very slightly curved toward the posterior petal, anthers 1.7–2 mm long, glandular connectives 1–1.2 mm long. Pollen grains 42 μm. Filaments of the anterior and anterior-lateral staminodes ca 3.4 mm long, posterior-lateral filaments ca 3 mm long, inflexed between the posterior styles, anterior and anterior-lateral glands 1.3–1.4 mm long, 1.2–1.3 mm wide, posterior-lateral glands ca 1.1 mm long, ca 0.8 mm wide, all glands with the apex and abaxial face smooth. Anterior style ca 3.2 mm long, ca 0.4 mm wide, slightly arced toward the posterior petal, posterior styles ca 2.8 mm long, ca 0.3 mm wide, divergent, arced toward the posterior-lateral petals, stigmas 0.5–0.6 mm wide, capitate. Samara not seen.

Type. *Martius s.n.* Brazil. Minas Gerais: "Inter fruticeta ad praedium Ypa [Yha] provinciae Minas Geraea in Goyasanae confinibus. . ." (holotype M! fragment P-JUSS!).

This species is known only from the type, which was collected in northwestern Minas Gerais near the Goiás border (Fig. 6). Plants of *P. hirta* are densely golden pubescent. The hairs of the stem and vegetative branches and of the upper surface of the larger leaves have unusually long stalks, at least 0.5 mm long and commonly 1 mm or more long. Such hairs are also found in *P. gardneri* of the southern part of the Chapada das Mangabeiras of northeastern Goiás. That species differs from *P. hirta* in its larger flowers in which the petal limbs are orbicular. Its staminode glands are all equally long. In *P. hirta* the limb of the posterior petal is obovate. The anterior and anterior-lateral staminode glands are longer than the posterior-lateral two. *P. anadenanthera* of central Goiás also

has long-stalked hairs, but is easily recognized by its anthers, which lack the glandular connective.

15. Peixotoa hispidula Adr. Jussieu, Ann. Sci. Nat. Sér. II, Bot. **3**: 279. 1840. Fig. 17.

P. hispidula f. 1. *subtomentosa* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 41. 1912. Type. *Gaudichaud 964* (lectotype G!, isotype P!).

P. hispidula f. 2. *subglabrata* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 41. 1912. Type. *Martius 1169 (lectotype G!, isotypes BM!* BR! F! GH! K! LE! M! MO! NY! P! S! W!).

P. hispidula f. 3. *micrantha* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 41. 1912. Type. *Salzmann 93* (holotype B, destroyed; isotype G!).

Erect, scandent or prostrate shrub or subshrub or vine. Vegetative branches loosely velutinous or sparsely so or glabrous when young, older parts glabrous or glabrate. Stem stipules 3.4–13 mm long, 3–11 mm wide, cordate or sometimes triangular, entire with apex acute or notched, or rarely bifid, finely velutinous or tomentulose or glabrous adaxially, sericeous, velutinous or tomentulose, or velutinous-tomentulose abaxially or only on the margins, or glabrous abaxially, usually deciduous, sometimes persistent; inflorescence stipules like the cauline but usually more densely pubescent, eventually deciduous. Stem leaves with the petiole 2–16 mm long, loosely, sparsely or densely, velutinous, sometimes glabrous, lamina 2.3–12 cm long, 1.5–7.3 cm wide, elliptical or ovate, sometimes lanceolate, oblanceolate or orbicular, apex apiculate, base cordate or slightly so, rarely almost truncate, glabrous or glabrate or sparsely sericeous or velutinous or sparsely so above, glabrous or glabrate or loosely or sparsely pubescent with T-shaped hairs or loosely or sparsely tomentose below, a pair of sessile glands at the base at the costa or halfway on the petiole or on the petiole up to 0.5 mm below the lamina or on the surface of the lamina up to 1.5 mm above the base, up to 0.5 (–2.3) mm from the costa, each gland 0.3–1.6 mm in diameter. Inflorescence leaves with the petiole at least 2 mm long, laminas abruptly smaller than the cauline, the smallest not less than 3.9 mm long, 1.2 mm wide, elliptical or lanceolate or linear-lanceolate or linear, apex acuminate to caudate, finely velutinous or sparsely sericeous to glabrate above, sericeous or sparsely so below, a pair of glands at the base at the costa or halfway on the petiole or sometimes on the petiole just below the lamina, each gland (0.2–) 0.4–1.3 (–1.8) mm in diameter, rarely with a second, smaller pair (ca 0.4 mm in diameter) just below the larger pair. Inflorescence terminal or axillary, the axes usually sparsely velutinous, sometimes sparsely tomentulose, internodes of the primary axis 0.5–5.3 cm long, 2° axes 0.9–4 cm long, 3° axes 1.3–3.2 cm long, commonly the inflorescence with one terminal umbel only or with 2° axes only, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary peduncles absent, secondary peduncles rare, up to 0.5 mm long. Bracts 0.4–1.5 mm long, 0.2–0.5 mm wide, triangular or oblong or linear, glabrous, or sometimes velutinous or tomentose abaxially and/or on the margins; bracteoles 0.1–0.3 mm long, 0.1–0.2 mm wide, triangular or semicircular, glabrous, or bracteoles absent. Pedicels 17–39 mm long, finely or sparsely velutinous, usually a little longer in fruit. Sepals 4.2–6 mm long, 1.2–3 mm wide, adaxially glabrous and the extreme apex tomentulose or the proximal 1/2–4/5 glabrous, the distal 1/2–1/5 tomentulose, glands 1.5–2.5 mm long, 0.6–1.2 mm wide. Claw of the lateral petals 2–3 mm long, limb 13–16 (–20) mm long, 11.5–15 (–18) mm wide, orbicular or broadly elliptical, base attenuate, fimbriae up to 0.5 mm long, glandular. Claw of the posterior petal 4.7–6.6 mm long, limb 6.5–8.2 mm long, 5–7 mm wide, elliptical, sometimes orbicular, fimbriae up to 0.6 mm long, capitate-glandular. Lateral stamen filaments 3.6–5 mm long, posterior filament 2.6–3.3 mm long, usually at

least slightly curved toward the posterior petal, sometimes erect, anthers 1–1.4 mm long, glandular connectives 0.8–0.9 mm long. Pollen grains ca 50 μm. Anterior and anterior-lateral staminode filaments 3.7–5.3 mm long, commonly the anterior filament a little longer than the anterior-lateral two or the three subequal, posterior-lateral filaments 2.4–3.7 (–4.5) mm long, always shorter than the anterior three, slightly curved toward the posterior styles, glands of the anterior and anterior-lateral staminodes 1.1–1.3 mm long, 1.3–1.7 mm wide, always wider than long, posterior-lateral glands 0.8–1.2 mm long, 0.7–1.2 mm wide, the anterior three with a deep or shallow indentation across the apex and decurrent on the abaxial face, posterior-lateral glands smooth. Anterior style (3.4–) 3.7–4.8 mm long, 0.3–0.4 mm wide, longer or shorter but always a little stouter than the posterior two, arced toward the posterior petal, posterior styles (3.7–) 4–5.2 mm long, 0.2–0.3 mm wide, divergent, slightly curved toward the anterior-lateral or posterior-lateral petals, stigmas 0.3–0.4 (–0.5) mm in diameter, capitate. Carpophore up to 3 mm long. Torus up to 5.3 mm high. Samara with the dorsal wing 1.7–2.4 cm long, 0.98–1.6 cm wide, upper margin straight or gently sigmoid, lower margin straight in the proximal ½–⅔, the distal ⅓–½ arced, slightly erose, lateral wings 2–3.3 (–5.5) mm wide, 6–10 mm high, rectangular, erose or irregularly dentate, areole 3.5–5.2 mm long, 3.2–4.2 mm wide, nut ca 4–6.5 mm long, 2.5–3.8 mm in diameter, seed 6.5–7.1 mm long, outer cotyledon 7.6–8.9 mm long, 2.2–2.4 mm wide, folded at ca ⅔ of its length, inner cotyledon 5.3–6.2 mm long, 1.5–2.2 mm wide, folded at ca ⅔–¾ of its length.

Type. *Martius 1169*. Brazil. Rio de Janeiro: Between Cabo Frio and Espírito Santo [fide Niedenzu, 1912]. 1841 (Lectotype P!, isotypes BM! BR! F! G! GH! K! LE! M! MO! NY! S! W!).

Distribution. (Fig. 6). Along the coast from Bahia to Rio de Janeiro, two collections from São Paulo; restingas, dunes, beaches.

BRAZIL. Bahia: Mun. Maraú, 4 km S of Maraú, *Almeida 136* (CEPEC); Maraú, *Belém 3456* (CEPEC, MICH, NY); Salvador, Lagôa de Abaeté, *Belém & Mendes 290* (IAN, NY, UB, US); *Blanchet 1908* (G), *116* (W); Itapaba, at Lagôa do Abaeté, E of Salvador, 10–20 m, *Davis 61059* (E); Porto Seguro, *Duarte 5966* (MICH); 5 km SE of Maraú at junction with new road N to Ponta do Mutá, 14°08′S, 39°00′W, 0–50 m, *Harley et al. 18510* (MICH); Ilhéus, *Riedel 617* (A, LE, S); *Salzmann 93* (G); *Wawra & Maly 142* (W). Espírito Santo: Mun. Serra, entre Nova Almeida e Santa Cruz, *Araujo 311 & Peixoto 181* (RB); Guarapari, *Duarte 3655, 4173* (RB), *Occhioni 7226* (MICH); inter Cabo Frio et Espírito Santo, *Wied-Neuwied s.n.* (BR). Rio de Janeiro: Rio de Janeiro, *Gaudichaud 963* (F, P, P-JUSS, RB, syntype of *P. hispidula*), *964* (G, P), *Lund 477c* (C, GOET); restinga de Itapú, *Araujo 690 & Peixoto 492* (MICH, RB); restinga de Piratininga, *Brade 12014* (R); Sarangiros dans les bois des Priner, *Glaziou 11819* (P); Lagôa de Piratininga, *Kuhlmann s.n.* (RB 26272); Santa Rosa, *Netto 88* (R); restinga de Aramama, *Occhioni s.n.* (RB 26440); restinga da Marambaia, *Occhioni 3554, 4313* (MICH); restinga de Itaipú, *Schwacke 7130* (NY, R); entre Macaé e Rio das Ostras, BR-6, Km 161, *Trinta 966 & Fromm 2042, Trinta 966-A & Fromm 2042-A* (R); Cabo Frio, *Alston-Lutz 56, 57* (R), *Fromm et al. 1334* (R), *Lindeman 6327* (MICH), *Markgraf 3047 & Brade* (RB), *Mello Filho 1129* (R), *Moreira & Angosto s.n.* (R 72184), *Netto et al. s.n.* (R 19558), *Restinga I-324* (GH, R, US), *I-765* (US), *I-1232* (US), *I-1233* (NY), *Riedel & Luschnath s.n.* (LE), *Segadas & Vianna 4210* (P), *Smith 6570* (R, US), *Sucre 3853, 4921* (MICH), *Ule 4706* (R), *Vidal s.n.* (R 39291); Recreio dos Bandeirantes, *Krapovickas et al. 23197* (F, G, MICH, MO, P), *Lutz 653* (R), *Markgraf 3788 & Brade* (RB), *Mello Filho 830, 980, 981* (R), *Pereira 10525* (M), *Rente 2, 238* (R), *Rodrigues 92* (R), *Santos 5086, 5087, 5088* (R), *Smith 6367* (NY, R, S, US); Restinga de Jacarepaguá, *Araujo 119* (MICH), *124* (RB), *140* (MICH), *Atala 80, 90* (R), *Berg 243* (U), *Brade 11003, 11396* (R), *Cuatrecasas & Duarte 26636 p.p.* (US), *Maas & Carauta 3129* (MICH), *Montalvo 17A* (RB), *Pereira 3569* (RB), *Vianna 135* (NY), *537* (MICH); Mun. Maricá, 2 km from "Amaral Peixoto," *Anderson 11650, 11653* (MICH), Lagôa de Maricá, *Occhioni 6389* (MICH), *Vidal V-100* (R); Praia Grande, Taipú, *Glaziou 1328* (BR, C, P), *3891* (C, F, K, P, R), *11815* (K, LE, US), *Riedel & Luschnath 1304* (LE, S, US); Restinga da Barra da Tijuca, *Anderson 11196* (MICH), *Calvano 11* (R), *Flaster 35* (R), *Kuhlmann 6221* (RB), *Machado 48* (MICH), *Medeiros 15* (MICH), *Miquel et al. 1* (MICH), *Occhioni 650* (MICH), *1153* (RB), *3675* (MICH), *Pereira 55* (R), *536* (MICH), *576* (RB), *Pimentel 14 & Barbosa 15* (RB), *Schott 3677* (W), *Trinta 542 & Fromm 1618* (R, M), *Trinta et al. 1386* (R), *Vianna 15* (R). São Paulo: São Paulo, *Frazão s.n.* (RB 11700); Mogu-guacú [Moji-Guaçu], *da Silva Manso s.n.* (*Lhotzky 257*) (BR).

One of the few well-collected species, *P. hispidula* is characterized by its large-flowered but small inflorescences. These are commonly composed of one terminal umbel and one or two pairs of secondary branches, each of which bears one terminal umbel only, or of a solitary umbel. 3° axes are rare. The flowers are among the largest in the genus. The limb of the lateral petals varies from ca 13 to 20 mm in diameter. The limb of the posterior petal is about half as long and wide as the limbs of the lateral petals. The staminode glands are strongly dimorphic. The anterior and anterior-lateral glands are wider than long, a condition unique in the genus, and have an indentation across the apex and decurrent on the abaxial face. The posterior glands are smaller, as long as wide, and smooth. The inflorescence leaves are relatively large, mostly lanceolate or narrowly elliptical, and with a petiole commonly 4–6 mm or more long.

Peixotoa hispidula is highly variable in habit and density of pubescence. In open areas it forms shrubs or subshrubs with erect, ascending or procumbent branches. Like many other species, it turns into a vine or climber if suitable support from adjacent shrubs and small trees is available. While the vegetative parts are usually glabrous or at most very sparsely pubescent, in some individuals the branches may be velutinous and the leaves velutinous above and sparsely tomentose below. This variation occurs throughout the range and does not merit infraspecific recognition.

The pubescent *P. axillaris,* of south-central Goiás, is the only other species with an inflorescence of one or three umbels. It differs in its smaller flowers whose staminode glands are subequal and smooth. *P. glabra,* from central Minas Gerais, is sometimes confused with *P. hispidula,* but is easily distinguished. It has larger inflorescences, whose distal leaves are sessile or subsessile, and subequal staminode glands.

Collected in flower and fruit throughout the year.

16. Peixotoa irwinii C. Anderson, sp. nov. Fig. 14.

Suffrutex; caules procumbentes vel ascendentes usque ad 2 m. Stipulae vegetativae 7–8 mm longae, acutae vel bifidae, deciduae. Petioli 4.5–5.5 mm longi. Laminae 6.3–9.5 cm longae, 3.7–5.6 cm latae, ellipticae vel anguste ovatae, rugosae, supra sparsim aureo-velutinae, subtus in venis ferentes pilos T-formes, basi juxta costam biglandulosae. Folia inflorescentiae petiolo brevi vel sessilia, linearia vel subulata. Inflorescentia terminalis, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 17–26 mm longi. Sepala 3.8–4 mm longa. Limbus petalorum lateralium 8.2–9 mm longus, obovatus, margine glanduloso-fimbriato. Limbus petali postici 5.2–5.8 mm longus, obovatus, margine glandulis capitatis ornato. Glandulae 3 staminodiorum anticorum late sed non profunde indentatae in pagina abaxiali. Styli subaequales, 4.1–4.2 mm longi, anticus arcuatus versus petalum posticum, postici divergentes, parum inclinati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Prostrate or ascending subshrub to ca 2 m. Vegetative branches coarsely golden velutinous, older parts glabrous. Stem stipules 7–8 mm long, 8–9 mm wide, cordate, entire with the apex acute or notched, or bifid, finely tomentulose adaxially or pubescent only in the distal ½, the proximal ½ glabrous, coarsely golden velutinous-sericeous abaxially, deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 3.6 mm long, ca 2.5 mm wide, the most distal sometimes split into two narrow, acute lobes, persistent. Stem leaves with the petiole 4.5–5.5 mm long, coarsely golden velutinous, laminas 6.3–9.5 cm long, 3.7–5.6 cm wide, elliptical or narrowly ovate, apex apiculate, base cordate, rugose, very sparsely golden velutinous

above, very sparsely pubescent with golden T-shaped hairs on the major veins only below, a pair of sessile glands at the base at the costa, each gland 1–1.5 mm in diameter. Inflorescence leaves of the proximal nodes petiolate, the more distal subsessile or sessile, laminas abruptly smaller than the cauline, the smallest not less than 3.2 mm long, 0.4 mm wide, linear or subulate, apex acuminate, finely velutinous above, sericeous or sericeous-velutinous below, a pair of glands at the base at the costa, each gland 1–1.7 mm in diameter, sometimes the most distal leaves reduced to eglandular, subulate bracts. Inflorescence terminal, the axes coarsely golden velutinous, internodes of the primary axis 3–4.5 cm long, 2° axes 0.9–4.8 cm long, 3° axes 1.3–2 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.5–1 mm long, 0.3–0.4 mm wide, linear or narrowly triangular, glabrous or sometimes sparsely velutinous on the margins; bracteoles 0.1–0.3 mm long and wide, triangular or oblong, glabrous. Pedicels 17–26 mm long, densely golden velutinous. Sepals 3.8–4 mm long, 2.2–2.6 mm wide, adaxially the proximal ⅓ glabrous, the distal ⅔ tomentulose, glands 1.4–1.6 mm long, 0.9–1 mm wide. Claw of the lateral petals 1.8–2.3 mm long, limb 8.2–9 mm long, 7–8.7 mm wide, obovate, base briefly attenuate, fimbriae up to 0.3 mm long, glandular. Claw of the posterior petal 4–4.2 mm long, limb 5.2–5.8 mm long, 4.3–4.5 mm wide, obovate, fimbriae up to 0.3 mm long, capitate-glandular. Filaments of the lateral stamens 3.5–4 mm long, posterior filament 3.4–3.5 mm long, very slightly curved toward the posterior petal, anthers 1–1.3 mm long, glandular connectives 0.6–0.7 mm long. Pollen grains 47–50 μm. Filament of the anterior staminode 3.7–4 mm long, arced toward the posterior petal, anterior-lateral filaments 3.4–3.8 mm long, posterior-lateral filaments 3–3.2 mm long, curved toward the posterior styles, anterior gland 1.1–1.2 mm long and wide, anterior-lateral glands 1–1.1 mm long and wide, posterior-lateral glands 0.9–1 mm long and wide, all glands with the apex smooth, anterior and anterior-lateral glands with a broad and shallow indentation on the abaxial face, posterior-lateral glands smooth. Styles 4.1–4.2 mm long, anterior style ca 0.4 mm wide, arced toward the posterior petal, posterior styles ca 0.3 mm wide, very slightly divergent, slightly inclined toward the posterior-lateral petals, stigmas ca 0.5 mm in diameter, capitate. Samara not seen.

Type. *Irwin et al. 28236b.* Brazil. Minas Gerais: Serra do Espinhaço, ca 3 km N of São João de Chapada, 1200 m, 24 Mar 1970 (holotype UB, isotype NY).

Peixotoa irwinii is known only from the type (Fig. 6). It is one of the few sparsely pubescent species in the genus, and is known only from the Serra do Espinhaço of Minas Gerais. *P. glabra* and sparsely pubescent forms of *P. reticulata* also occur in the Serra do Espinhaço, but are readily distinguished from *P. irwinii.* The anterior and anterior-lateral staminode glands of *P. irwinii* are unique in that, though the apex of each gland is smooth, the abaxial face has a shallow depression. Its petioles are golden velutinous, the limbs of the lateral petals are obovate, and the styles are subequal. In *P. glabra* the anterior and anterior-lateral staminode glands have an indentation across the apex and decurrent on the abaxial surface, the petioles are glabrous, the limbs of the lateral petals are orbicular, and the styles are unequal. *P. reticulata* has smooth staminode glands and larger petals. The limbs of its lateral petals are ca 12–15 mm long and wide. The limb of its posterior petal is ca 8–12 mm long and wide. The limbs of the lateral petals of *P. irwinii* are 8.2–9 mm long and 7–8.7 mm wide. The limb of the posterior petal is 5.2–5.8 mm long, 4.3–4.5 mm wide.

This species is named for Howard S. Irwin in recognition of his extensive collecting efforts in the Planalto of Brazil.

17. Peixotoa jussieuana Adr. Jussieu, Ann. Sci. Nat. Sér. II, Bot. **13**: 279. 1840. Fig. 12.

P. jussieuana var. *β velutina* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 36. 1912. Type. *Gardner 2067* (lectotype G!, isotypes F! GH! K! P! W!).

Ascending shrub or vine to ca 0.8 m. Vegetative branches loosely or densely velutinous, pubescence abraded from older parts. Stem stipules ca 6–8 mm long, ca 6–7 mm wide, cordate-triangular, apex acute, glabrous adaxially, loosely sericeous-tomentulose abaxially, deciduous; inflorescence stipules 6–ca 9 mm long, 5.3–ca 9 mm wide, cordate or cordate-triangular, finely or sparsely velutinous adaxially, sericeous-tomentulose abaxially, deciduous. Stem leaves with the petiole 2.5–9 mm long, loosely or densely velutinous or velutinous-tomentose, laminas 6–13 cm long, 3–7.5 cm wide, ovate or lanceolate, often the distal ⅓ attenuated toward the apiculate apex, base cordate or nearly truncate, sparsely or densely velutinous above, loosely, sparsely or densely pubescent with T-shaped hairs, rarely tomentose, below, a pair of sessile glands at the base at the costa or halfway on the petiole or on the surface of the blade up to 4 mm above the base, up to 5 mm from the costa, each gland 0.5–1.5 mm in diameter, sometimes one or both glands absent. Inflorescence leaves with the petiole 0.5 mm or more long, laminas abruptly smaller than the cauline, the smallest not less than 2.7 mm long, 1 mm wide, shape of the more proximal like the cauline, the more distal linear-lanceolate or linear, apex acuminate, velutinous or sparsely so or sparsely tomentulose or the most distal sometimes glabrous adaxially, densely pubescent with T-shaped hairs abaxially, a pair of glands at the base at the costa or halfway on the petiole, each gland 0.3–1.5 mm in diameter. Inflorescence terminal or axillary, the axes velutinous or tomentulose-velutinous, internodes of the primary axis 0.4–6.5 cm long, 2° axes 0.5–9 cm long, 3° axes 0.4–2.7 cm long, 4° axes 0.4–1.6 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.2–0.7 (–3) mm long, 0.2–0.5 (–1.2) mm wide, triangular or semicircular, glabrous; bracteoles 0.1–0.3 (–0.5) mm long, 0.1–0.2 mm wide, triangular, glabrous; sometimes bracts and bracteoles absent. Pedicels 9–18 mm long, velutinous or velutinous-tomentulose, sometimes a little longer in fruit. Sepals 4.8–6 mm long, 2.5–3 mm wide, adaxially the proximal ¼–½ glabrous, the distal ¾–½ velutinous, glands 1.5–2.5 mm long, 0.7–1.3 mm wide. Claw of the lateral petals 2–2.3 mm long, limb 10.5–12 mm long, ca 9–10 mm wide, obovate, base attenuate, fimbriae up to 0.9 mm long, glandular. Claw of the posterior petal 4.2–4.5 mm long, limb 7.5–8 mm long, ca 6 mm wide, obovate or elliptical, fimbriae up to 0.5 mm long, those of the proximal ⅔ capitate-glandular, the distal ⅓ fimbriate-glandular. Lateral stamen filaments 5.5–7 mm long, the distal 1/5–1/7 of the anterior-lateral two curved toward the posterior petal, posterior filament 4.4–5 mm long, strongly arced toward the posterior petal, anthers 1.2–1.4 mm long, glandular connectives 0.8–1 mm long. Pollen grains ca 50 μm. Anterior staminode filament 5.5–6.2 mm long, always exceeding the anterior-lateral two, anterior-lateral filaments 4.5–5.8 mm long, always exceeding the posterior-lateral two, posterior-lateral filaments 4–5.3 mm long, inflexed between the posterior styles, glands 1–1.4 mm long, 0.9–1.2 mm wide, the anterior gland sometimes a little larger than the other four, the posterior-lateral glands sometimes a little narrower than the anterior three, all with the apex and abaxial face smooth. Styles (5–) 5.2–6.5 mm long, 0.3–0.4 mm wide, often the anterior a little longer or sometimes a little shorter but always a little stouter than the posterior two, anterior style strongly arced toward the posterior petal, the stigma oblong, ca 0.4 mm long, borne laterally at the apex on the abaxial surface or very rarely capitate and the style sharply hooked at the apex, posterior styles divergent, the

distal 1/5–1/6 curved toward the posterior-lateral petals, all styles with scattered hairs in the proximal ¼–⅓ of their lengths, stigmas capitate, ca 0.4 mm in diameter. Carpophore up to 2.3 mm long. Torus up to ca 4 mm high. Samara with the dorsal wing ca 2 cm long, ca 1.1 cm wide, upper margin arced, lower margin straight in the proximal ⅓, the distal ⅔ curved, erose, lateral wings 7–9 mm wide, 9–11 mm high, rectangular, extending up to ca 7 mm below the nut, erose, areole 3.5–4 mm long, 3.5–3.6 mm wide, nut ca 5 mm long, ca 4 mm in diameter, mature seed not seen.

Type. *Martius s.n.* Brazil. Maranhão: "In sylvis sepibusque ad fluv. Itapicurú prope Caxias . . ." June [1819] (lectotype M! fragment P-JUSS!, isotype M!).

Distribution. (Fig. 7). Ceará, Piauí, and Maranhão, one collection from Paraná; caatingas, woodlands, and at forest margins.

BRAZIL. Ceará: *Allemão & Cysneiros 214* (R); Serra da Ibiapaba, *Mello s.n.* (RB 67422). Maranhão: Mun. Lorêto, "Ilha de Balsas" region, ca 45 km S of Lorêto, 7°26′S, 45°0′W, 250–300 m, *Eiten & Eiten 4835* (SP, US); Grajaú, *Lisbôa 2506* (MG). Paraná: Mun. Paranaí, estrada Paranaí-Panelas, *Hatschbach 1413* (MICH, RB). Piauí: Mun. Picos, ca 30 km E of Picos, 7°7′S, 41°9′W, *Eiten & Eiten 4917* (US); between Boa Esperança and Santa Ana das Mercês, *Gardner 2067* (BM, F, G, GH, K, P, W); Lagôa Comprida, *Gardner 2498* (BM, K); Oeiras, *Jobert 1045, 1053* (P, R); Chapada de Bom Jesus, *Lützelburg 275* (M), *1721* (RB); São João do Piauí, *Lützelburg 1599* (RB); Oeiras, *Martius s.n.* (M, P-JUSS, syntype of *P. jussieuana*); Serra Branca, *Ule 7446* (G, K).

In *P. jussieuana* the anterior style is strongly arced toward the posterior petal and bears an oblong stigma at the apex but laterally on the abaxial surface. The only other species with such an anterior stigma is *P. magnifica* from central and southern Goiás, Mato Grosso and eastern Bolivia. It is probably a close relative. It differs in that its stipules are larger (12–23 mm long), and in that the limbs of its lateral petals are orbicular. The samaras of *P. magnifica* have semicircular lateral wings 10.5–20 mm high. In *P. jussieuana* the stem stipules are ca 6–8 mm long and the lateral petal limbs are obovate. The lateral wings of the samara are rectangular and 8–11 mm high. The leaves of *P. jussieuana* are at times attenuated in the distal one-third.

A surprising disjunct is *Hatschbach 1413* from eastern Paraná. This collection is also atypical in that the tip of the anterior style is uncinate and bears a capitate stigma. Some intermediates between this peculiar style and the usual condition have been noted in some of the flowers. It is unlikely that the specimens labeled *Glaziou 9680* were actually collected in Rio de Janeiro.

This species was named by Martius in honor of Adrien de Jussieu, who published it.

Collected in flower from January through August, in fruit in January and in May through July.

18. Peixotoa leptoclada Adr. Jussieu, Ann. Sci. Nat. Sér. II, Bot. **13**: 279. 1840. Fig. 16.

P. jussieuana var. α *glabrescens* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 36. 1912. Type. *Mendonça 976* (lectotype, NY!)

Vine or scandent shrub. Vegetative branches tomentulose-velutinous, the older parts glabrous. Stem stipules 10.5–20 mm long, 11–18 mm wide, triangular or broadly cordate, entire with the apex acute or notched, or bifid, finely velutinous or sericeous-velutinous or glabrate adaxially, tomentulose or sericeous-velutinous abaxially, persistent or deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 7 mm long, 7.7 mm wide, or sometime equal to or larger than the cauline, entire with the apex acute or notched, or bifid, more densely pubescent than the cauline, persistent. Stem leaves with the petiole 5–20 mm long, densely golden

velutinous, laminas 6–17.5 cm long, 3–11 cm wide, elliptical or lanceolate or, especially the larger, ovate, apex apiculate, base cordate or almost truncate, golden velutinous above, loosely tomentose or pubescent with T-shaped hairs below, a pair of sessile glands at the base at the costa or on the surface of the lamina up to 4 mm above the base, up to 9 mm from the costa, or sometimes halfway on the petiole, often with a second pair borne on the surface of the lamina, 0.6–17 mm above the base, up to 15 mm from the costa, each gland (0.6–) 0.9–1.8 mm in diameter. Inflorescence leaves with the petiole 0.6 mm or more long, very rarely the most distal sessile, laminas abruptly smaller than the cauline, the smallest not less than 1.3 mm long, 0.4 mm wide, lanceolate or oblanceolate or linear or subulate, apex acuminate and sometimes with a tiny gland, velutinous above, the most distal glabrous above, densely sericeous or velutinous below, a pair of glands at the base at the costa or halfway on the petiole, sometimes the glands obliquely stalked, each gland ca 0.4–1.2 mm in diameter, the larger laminas often with a second, smaller pair of glands (0.3–0.5 mm in diameter) borne on the surface of the lamina or adjacent to or just above or just below the larger pair; sometimes the most distal leaves reduced to sessile, subulate, eglandular bracts, 2.7–3.5 mm long, 0.6–0.8 mm wide. Inflorescence terminal or axillary, the axes velutinous, internodes of the primary axis 1–9.3 cm long, 2° axes 0.8–16.7 cm long, 2° subsidiary axes 2–2.3 cm long, 3° axes 0.8–3.3 cm long, 4° axes 0.9–1 cm long; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.2–0.7 mm long, 0.2–0.3 mm wide, narrowly to broadly triangular or semicircular, glabrous, sometimes velutinous or tomentulose abaxially and/or on the margins; bracteoles 0.1–0.3 mm long, 0.1–0.3 mm wide, triangular, glabrous, sometimes the margins velutinous. Pedicels 17–24 (–31) mm long, velutinous or velutinous-tomentulose. Sepals 4.8–6 (–7) mm long, 2.5–3.5 mm wide, adaxially glabrous or the apex tomentulose or the proximal ½–⅔ glabrous, the distal ½–⅓ sparsely velutinous, glands 1.8–2.6 mm long, 1–1.5 mm wide. Claw of the lateral petals 2.5–3.2 mm long, limb 11–14 mm long, 10.8–13.7 mm wide, orbicular or broadly obovate, base briefly attenuate, fimbriae up to 0.8 mm long, glandular. Claw of the posterior petal 3.7–4.5 mm long, limb (7–) 7.5–10.5 mm long, (5.2–) 5.8–9.2 mm wide, obovate or broadly so, fimbriae up to 0.6 mm long, capitate-glandular, glands of the apex a little smaller. Filaments of the lateral stamens 4.5–5.2 mm long, posterior filament 4.2–4.5 mm long, always shorter than the lateral four, arced toward the posterior petal, anthers 1.2–1.6 mm long, glandular connectives 0.5–0.9 mm long. Pollen grains 42–50 μm. Filaments of the staminodes (3.2–) 4.1–4.8 mm long, sometimes the anterior a little longer than the lateral four, posterior-lateral filaments inflexed between the posterior styles, glands 1.2–1.5 mm long, the anterior usually a little longer than the other four, anterior and anterior-lateral glands 1.3–1.4 mm wide, posterior-lateral glands 1.1–1.2 mm wide, all glands with the apex and abaxial face smooth. Anterior style (4.3–) 4.7–5 mm long, 0.4–0.5 mm wide, arced toward the posterior petal, posterior styles (4.5–) 5–5.3 mm long, 0.3–0.4 mm wide, always exceeding the anterior style, divergent, arced toward the posterior-lateral petals, all styles velutinous in the proximal 1/5 of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Mature samara not seen.

Type. *Claussen s.n.* Brazil. Minas Gerais. "In sylvis post incendia redivivis (vulgo capueiras) . . ." (holotype P-JUSS!, isotype P!).

Distribution. (Fig. 7). Central Minas Gerais and south-central Goiás; woodlands and gallery forests.

BRAZIL. Goiás: Serra dos Pirineus, ca 15 km (str. line) N of Corumbá de Goiás, 1250–1300 m, *Anderson 10222* (MICH, NY, UB); Fazenda do Palmital, *Glaziou 20749* (BR, C, G, L, P, R); Luziânia, Rio Vermelho a 15 km de cidade, *Heringer 17258* (MICH); Allegrio, *Pohl 2946 (1563d)* (F, K NY, W). Minas Gerais: *Claussen 522* (C, F, GH, P, S), *Claussen 643* (G), *Claussen s.n.* (F 1540004, 1540005), *Claussen s.n.* (G); *Mendonça 976* (NY); *Schwacke s.n.* (R 19578).

Peixotoa leptoclada is readily recognized by the large stipules, which are often persistent on the stem and always so at the more distal nodes of the inflorescence. *P. cordistipula* of Mato Grosso also has large, persistent inflorescence stipules but differs in its dense, white pubescence that gives the plants a silvery-grey appearance. Its leaves are usually densely tomentose below. The stem and leaf pubescence of *P. leptoclada* is moderate. In *P. cordistipula* the staminode filaments are unequal: the anterior exceeds the anterior-lateral two, and these exceed the posterior-lateral two. In *P. leptoclada* the staminode filaments are equal or the anterior may exceed the lateral four. The anterior style is longer than the posterior two in *P. cordistipula* but shorter in *P. leptoclada*. Another species with unusually large stipules is *P. hatschbachii* from central Goiás. It is easily distinguished by its glabrous stems and leaves and the stalked leaf glands. Some forms of *P. goiana* have large stipules but these are deciduous in the inflorescence. Also, the inflorescence leaves of *P. goiana* are sessile. Those of *P. leptoclada* are petiolate and often bear the glands slightly and obliquely stalked.

Peixotoa paludosa of central Minas Gerais and southern Bahia may be a close relative. Its inflorescence stipules, though smaller, are often persistent. It also has petiolate inflorescence leaves, similar staminodes, and an anterior style that is shorter than or subequal to the posterior two. It differs from *P. leptoclada* in that the leaf glands are borne on the surface of the lamina away from the base and costa. Such glands do occur sometimes in large leaves of *P. leptoclada* but usually in addition to a basal pair. The flowers of *P. leptoclada* are larger than those of *P. paludosa*.

No mature fruits are at hand, but immature samaras show that the dorsal and lateral wings are large and perhaps similar to those of *P. magnifica* and *P. jussieuana*. Samaras of *P. paludosa* also have wide lateral wings.

While the majority of collections seen are presumed to be sexual, *Anderson 10222, Glaziou 20749* and *Heringer 17258*, all from Goiás, are apomicts. The pollen, contained in closed anthers, is 81–83% non-staining in cotton blue in lactophenol. These specimens are noticeably more robust than the sexual plants; especially the inflorescence axes appear sturdier and less graceful than in the specimens that Jussieu saw.

19. Peixotoa magnifica C. Anderson, sp. nov. Fig. 19.

Frutex scandens vel liana usque ad 8 m. Stipulae vegetativae (10–)12–23 mm longae, cordatae vel triangulari-cordatae, acutae, deciduae, inflorescentiae interdum bifidae. Petioli (6.5–)8–28 mm longi. Laminae 7–28.2 cm longae, 4.7–14 cm latae, ovatae vel ellipticae vel anguste ellipticae interdum suborbiculares interdum obovatae, basi cordatae interdum parum cordatae raro obliquo-cordatae, supra aureo-velutinae, subtus ferentes pilos T-formes vel tomentosae, basi juxta costam biglandulosae interdum 3–4-glandulosae. Folia inflorescentiae petiolo brevi, distaliora anguste lanceolata vel triangularia vel linearia, acuminata vel caudata. Inflorescentia terminalis vel axillaris, umbellis singularibus. Bracteae bracteolaeque praesentes interdum absentes. Pedicelli (8–)17–27 mm longi. Sepala 5–8 mm longa. Limbus petalorum lateralium 15–17.8 mm longus, orbicularis, margine glanduloso-fimbriato. Limbus petali postici 9.5–12 mm longus, obtrapezoideus vel orbicularis vel late obovatus, margine glandulis capitatis ornato. Filamenta staminum antico-lateralium inclinata versus petalum posticum, filamentum staminis postici multum arcuatum versus petalum posticum. Styli subaequales vel saepius anticus quam postici longior vel raro brevior, anticus 7.3–9.2 mm longus, arcuatus versus petalum posticum, stigmate oblongo abaxiali, postici 7.5–9.2 mm longi, divergentes, arcuati versus petala postico-lateralia praesertim ¼ distali, stigmatibus capitatis. Ala dorsalis samarae 2.9–4.2 cm longa, 1.7–2.4 cm lata, alae laterales 7–10 (–12) mm latae, 10.5–20 mm altae, extensae usque ad 8 mm subter nucem.

Climbing or scandent shrub or vine to 8 m. Vegetative branches densely, usually golden, velutinous. Stem stipules (10–) 12–23 mm long, 8.8–22 mm wide, cordate or triangular-cordate, apex acute, velutinous adaxially, most densely so at the apex and base, velutinous-tomentose or velutinous abaxially, deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 5 mm long, 5 mm wide, cordate, concave, entire with the apex acute or apiculate, sometimes bifid, adaxially the proximal ¼–⅓ densely velutinous, the distal ¾–⅔ glabrous or sometimes very sparsely velutinous, abaxially densely velutinous-tomentose or sometimes only velutinous, deciduous or persistent. Stem leaves with the petiole (6.5–) 8–28 mm long, densely, usually golden, tomentose-velutinous, laminas 7–28.2 cm long, 4.7–14 cm wide, ovate or elliptical or narrowly so, sometimes suborbicular or obovate, apex apiculate, base cordate or slightly so, rarely oblique-cordate, golden velutinous above, usually loosely, sparsely, sometimes densely, pubescent with T-shaped hairs or tomentose below, a pair of sessile glands at the base at the costa or halfway on the petiole, rarely on the petiole just below the lamina, rarely borne on the surface of the lamina up to 0.9 mm above the base, up to 1.5 mm from the costa, each gland (0.7–) 1–2 mm in diameter. Inflorescence leaves with the petiole at least 1 mm long, laminas abruptly smaller than the cauline, the smallest not less than 2.3 mm long, 0.6 mm wide, the more proximal elliptical or narrowly so or oblanceolate, the more distal narrowly lanceolate or triangular or linear, apex acuminate or caudate, sparsely velutinous or glabrous above, densely velutinous below, a pair of glands halfway on the petiole or sometimes at the base at the costa, each gland 0.5–1.7 mm in diameter, sometimes with a second, smaller pair (0.4–0.7 mm in diameter) above or below the larger pair. Inflorescence terminal or axillary, the axes usually densely golden velutinous or velutinous-tomentulose, internodes of the primary axis 1.6–11 cm long, 2° axes (0.5) 1.5–17 cm long, 2° subsidiary axes 1.5–5.5 cm long, 3° axes 0.5–5.2 cm long, 4° axes 1.4–1.8 cm long; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.3–2.4 mm long, 0.1–0.6 mm wide, triangular or linear, glabrous, sometimes sparsely tomentulose abaxially and/or on the margins; bracteoles 0.1–0.6 mm long, 0.1–0.3 mm wide, triangular, glabrous; sometimes bracts and bracteoles absent. Pedicels (8–) 17–27 mm long, densely velutinous or velutinous-tomentose, usually golden, becoming up to ⅓ again as long in fruit. Sepals 5–8 mm long, 2.8–4.2 mm wide, adaxially the proximal 1/2–7/8 glabrous, the distal 1/2–1/7 velutinous or tomentulose, glands 2.1–3.7 mm long, 1–1.8 mm wide. Claw of the lateral petals (3–) 3.5–5.3 mm long, limb 15–17.8 mm long, 15–17 mm wide, base briefly attenuate or rarely truncate, fimbriae up to 1 mm long, glandular. Claw of the posterior petal 5–7.3 mm long, limb 9.5–12 mm long, 8–12 mm wide, orbicular or broadly obovate or obtrapezoidal, fimbriae up to 0.7 mm long, capitate-glandular. Filaments of the lateral stamens 6.5–8.4 mm long, the distal ¼ of the anterior-lateral two curved toward the posterior petal, posterior filament 5–5.6 (–6) mm long, strongly arced toward the posterior petal, anthers 1.4–2 mm long, glandular connectives 0.6–1.1 mm long. Pollen grains 60–63 μm. Filament of the anterior staminode (6–) 6.5–7.8 mm long, anterior-lateral filaments (4.8–) 5.5–6.5 mm long, posterior-lateral filaments (4–) 5–6.3 mm long, strongly inflexed between the posterior styles, glands (1–) 1.2–1.6 mm long, 1.2–1.5 mm wide, the posterior-lateral glands usually a little smaller than the anterior three, all glands with the apex and the abaxial surface smooth, rarely bearing 1 or 2 fertile locules, 0.7–1 mm long. Anterior style 7.3–9.2 mm long, ca 0.5 mm wide, strongly arced with especially the distal ¼ tapered and curved toward the posterior petal, the stigma oblong, 0.5–0.6 mm long, borne laterally at the apex on the abaxial surface, posterior styles 7.5–9.2 mm long, 0.4–0.5 mm wide, usually a little shorter than the anterior style, divergent, gently arced, especially the distal ¼, toward

the posterior-lateral petals, stigmas 0.4–0.5 mm in diameter, capitate, all styles usually with scattered hairs in the proximal ⅓ or less of their lengths. Carpophore up to 2.6 mm long. Torus up to 8 mm high. Samara with the dorsal wing 2.9–4.2 cm long, 1.7–2.4 cm wide, upper margin gently arced, lower margin usually falcate, entire or gently erose, lateral wings 7–10 (–12) mm wide, 10.5–20 mm high, semicircular, extending up to ca 8 mm below the nut, areole 4.5–7.8 mm long, 4.4–7 mm wide, nut 5–8 mm long, 5–7 mm in diameter, mature seeds not seen.

Type. *Anderson 9831*. Brazil. Mato Grosso: Ca 12 km ENE of Barra do Garças, ca 840 m, 6 May 1973 (holotype UB, isotypes MICH, NY).

Distribution. (Fig. 7). Southern Goiás, including the Distrito Federal, central and southwestern Mato Grosso, and eastern Bolivia; cerrado and woodlands.

BOLIVIA. Dept. Santa Cruz: Prov. Ñuflo de Chavez, Estancia Novicia, ca 30 km S de Concepción, 62°12′W, 16°29′S, 500 m, *Krapovickas & Schinini 32117* (CTES, MICH); Prov. Velasco, San Ignacio, 60°58′W, 16°22′S, 370 m, *Krapovickas & Schinini 32251* (CTES, MICH)); Prov. Velasco, 27 km S de San Ignacio, camino a San Miguel, 61°W, 16°36′S, ca 400 m, *Krapovickas & Schinini 32379* (CTES, MICH); Prov. Chiquitos, 3 km NW de Roboré, 59°46′W, 18°20′S, 300 m, *Krapovickas & Schinini 36399* (MICH); Prov. Velasco, *Kuntze s.n.* (NY). BRAZIL. Distrito Federal: entre Brasília e Niquelândia, *Pires et al. 9709* (UB, US). Goiás: ca 10 km by road W of Iporá, 600 m, *Anderson 9359* (MICH, NY, UB); Serra do Caiapô, ca 5 km (str. line) S of Caiapônia, 850 m, *Anderson 9474* (MICH, NY, UB); Serra Dourada, ca 17 km (str. line) S of Goiás Velho, 6 km NE of Mossamedes, 700–780 m, *Anderson 10162* (MICH, NY, UB); ca 5 km W of Niquelândia, ca 750 m, *Anderson et al. 35028* (MICH,

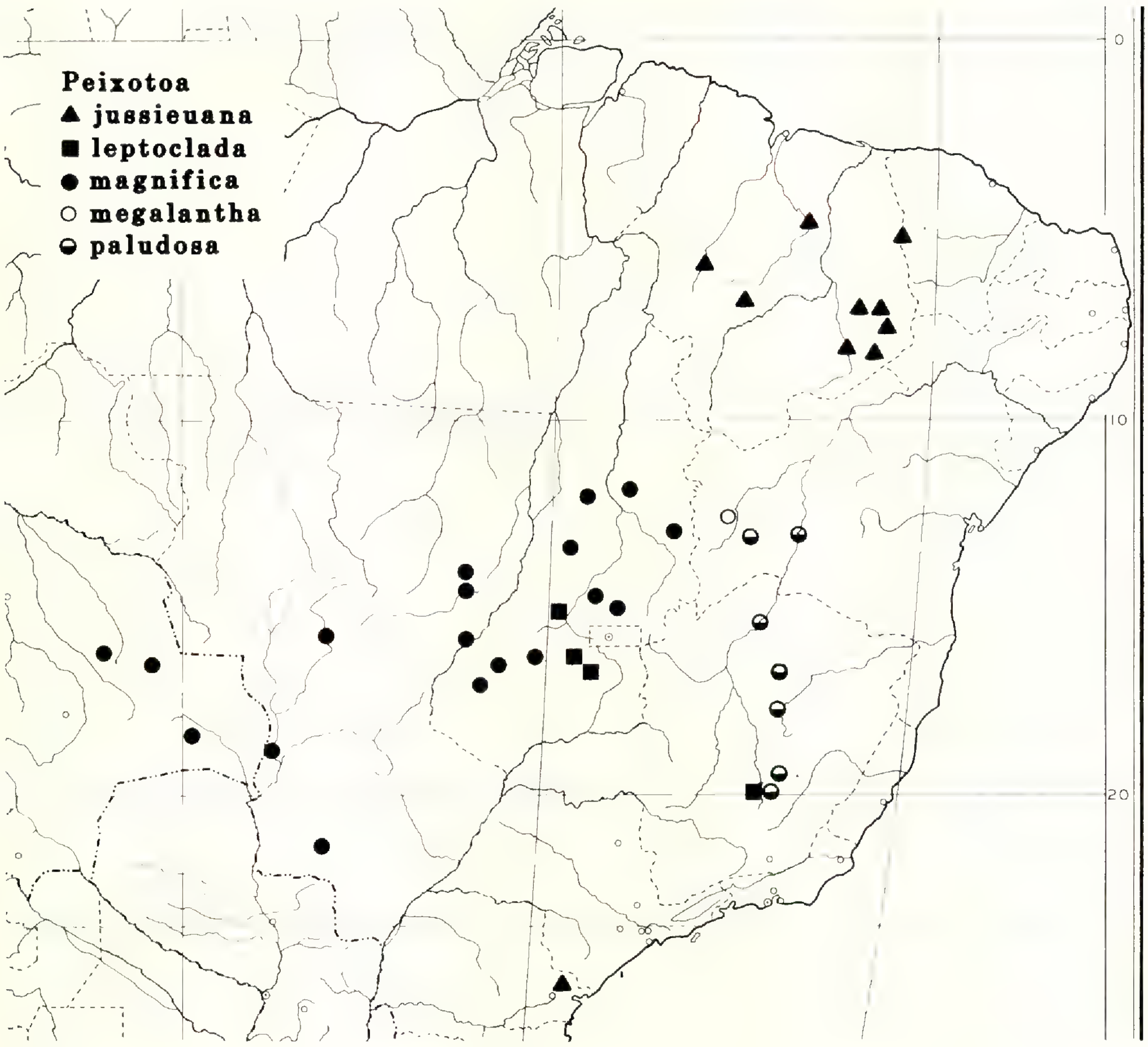

FIG. 7. Distribution of *P. jussieuana*, *P. leptoclada*, *P. magnifica*, *P. megalantha*, and *P. paludosa*.

NY); prope urbem Goyaz [Goiás], *Burchell 7133-2, 7084-2* (K); Serra Dourada, along affluent of the Rio Canna Brava, 28 km E of Formoso, 48°50′W, 13°45′S, *Dawson 15005* (LAM); Chapada dos Veadeiros, Pouso Alto, 1800 m, *Ferreira 215, 216, 217* (UB); Serra da Santa Brida [Brígida], *Gardner 3623* (K); Caiapônia, *Hatschbach 37700* (MICH); drainage of the upper Rio Araguaia, ca 70–87 km SE of Aragarças, 700 m, *Irwin et al. 17494* (MICH, NY, UB), *17554, 17631* (MICH, UB); Barra Pillar, Villa Boa [Goiás], *Pohl 1739, 3555 (1559d) p.p.* (K, W); vicinity of Estrela do Norte, Belém-Brásilia, *Prance & Silva 58433* (MICH, NY); Natividade, *Rizzo 9819* (MICH); Salinas, *Weddell 2024* (P). Mato Grosso: Serra do Roncador, mun. Barra do Garças, 250 km along new road NNE of Xavantina, ca 450 m, *Eiten & Eiten 9014* (NY, US); Vale do Sonho, Xavantina, acampamento da Fundação Brasil Central, *Fonseca 276* (NY, UB); Xavantina, *Harley & Souza 11037* (K, MO, NY, P, UB); Xavantina-Cachimbo road, 85 km from Xavantina, *Hunt 5700* (NY); neighborhood of Xavantina, *Hunt 5868* (NY); Serra do Roncador, ca 60 km N of Xavantina, 550 m, *Irwin et al. 15997* (MICH, NY, UB); Xavantina, 400 m, *Irwin et al. 16792* (MICH, NY, UB); Cuyabá [Cuiabá], *Malme 1610x* (S); Nioaque, *Ramamoorthy 618* (NY); ca 3 km S of Xavantina, 52°20′W, 14°44′S, *Ratter R112 p.p.* (K, UB); 1 km S of Xavantina, 52°20′W, 14°44′S, *Ratter & Ramos 370* (K, NY, P, RB, UB); Pantanal, Rio Paraguai, Fazenda Bela Vista, *Schaller 89* (NY); Urucum, Corumbá, 600 ft, *Smith 74* (K).

The usually large inflorescences of *P. magnifica* bear showy flowers most of which are open at about the same time. The unusual anterior style bears an oblong stigma at the apex but laterally on the abaxial surface. *P. jussieuana* from Ceará, Piauí and Maranhão is the only other species in the genus with such a stigma and is probably a close relative. It differs in that its lateral petals have obovate limbs while those of *P. magnifica* are orbicular. The samaras of *P. magnifica* have large, semicircular lateral wings that are recurved and give the fruit an inflated appearance. In *P. jussieuana* the lateral wings are rectangular and smaller. The cauline stipules of *P. magnifica* are 12–23 mm long while those of *P. jussieuana* are 6–8 mm long.

Peixotoa magnifica has often been assigned to *P. cordistipula* of central Mato Grosso and eastern Bolivia. They are readily separated on the basis of their styles. Those of *P. cordistipula* all bear the usual capitate stigma and are less than 5.5 mm long. The styles of *P. magnifica* are 7–9.2 mm long. Most striking in *P. cordistipula* are the large inflorescence stipules which persist even after the pedicels have been shed. While *P. cordistipula* also produces large inflorescences, only a few flowers are open at any one time. Its dense white pubescence gives the plants a silvery-grey appearance that is not evident in *P. magnifica*. A structure commonly found in *P. cordistipula* but absent in *P. magnifica* is a central, glandular mass in the umbel.

The staminode glands of *P. magnifica* rarely bear one or even two small locules that remain closed and contain largely aborted pollen.

Collected in flower and fruit from April through December.

20. Peixotoa megalantha C. Anderson, sp. nov. Fig. 21.

Frutex caulibus gracilibus usque ad 1.5 m. Stipulae vegetativae 16–23 mm longae, acutae vel bifidae, persistentes, interdum deciduae. Petioli 5–9.5 mm longi. Laminae 10.5–20 cm longae, 7–17.2 cm latae, late ellipticae vel ovatae, rugosae, supra juniores velutinae maturae glabrae, subtus tomentosae, basi juxta costam biglandulosae. Folia inflorescentiae petiolo brevi distaliora sessilia, linearia vel subulata. Inflorescentia terminalis, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 22–27 mm longi. Sepala 6.5–7.6 mm longa. Limbus petalorum lateralium 16–16.6 mm longus, orbicularis, margine glanduloso-fimbriato. Limbus petali postici 9.5–10 mm longus, late obovatus, margine glandulis capitatis ornato. Filamentum staminis postici erectum. Stylus anticus ca 5.2 mm longus, parum inclinatus versus petalum posticum, styli postici 5.4–5.5 mm longi, divergentes, arcuati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Shrub with slender stems to 1.5 m. Vegetative branches tomentose, pubescence abraded from older parts. Stem stipules 16–23 mm long, 14–20 mm wide,

cordate, entire with the apex acute, or bifid, glabrate or tomentulose adaxially, tomentulose-velutinous abaxially, persistent, sometimes deciduous; inflorescence stipules like the cauline, entire with the apex acute or notched, usually more densely pubescent, persistent. Stem leaves with the petioles 5–9.5 mm long, tomentulose-velutinous, laminas 10.5–10 cm long, 7–17.2 cm wide, broadly elliptical or ovate, apex apiculate, base cordate, rugose, the younger leaves velutinous above, the older leaves glabrous above, all tomentose below, a pair of sessile glands at the base at the costa or more commonly halfway on the petiole, each gland 1.6–3 mm in diameter. Inflorescence leaves with a small petiole at the more proximal nodes, the more distal sessile, laminas abruptly smaller than the cauline or gradually decreasing in size toward the distal nodes, the smallest not less than 4.5 mm long, 0.6 mm wide, shape of the more proximal like the cauline, the more distal linear or subulate, apex acuminate, finely velutinous above, tomentose-velutinous below, a pair of glands at the base at the costa, each gland ca 1–2 mm in diameter, sometimes with a second, smaller pair (ca 0.6 mm in diameter) above the larger pair. Inflorescence terminal, the axes tomentulose, internodes of the primary axis 3.8–9.8 cm long, 2° axes 3.6–6.3 cm long, mature 3° axes not seen, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.7–0.8 mm long, ca 0.7 mm wide, triangular, glabrous, sometimes tomentulose on the margins; bracteoles 0.4–0.5 mm long, 0.3–0.4 mm wide, triangular, glabrous. Pedicels 22–27 mm long, tomentose. Sepals 6.5–7.6 mm long, 3.5–4 mm wide, adaxially tomentulose-velutinous, glands 2.3–3.5 mm long, 1.5–1.7 mm wide. Claw of the lateral petals 2.5–2.8 mm long, limb 16–16.6 mm long, 15–16 mm wide, orbicular, base attenuate, fimbriae up to 1 mm, glandular. Claw of the posterior petal ca 5 mm long, limb 9.5–10 mm long, ca 9–9.5 mm wide, broadly obovate or suborbicular, fimbriae up to 0.9 mm long, capitate-glandular, glands of the distal ⅓ much smaller. Filaments of the lateral stamens 5–5.3 mm long, posterior filament 4.5–4.7 mm long, erect, anthers 1.6–1.8 mm long, glandular connectives 0.8–0.9 mm long. Pollen grains 63–74 μm. Filaments of the anterior and anterior-lateral staminodes 4.8–5 mm long, posterior-lateral filaments 4.4–4.5 mm long, inclined toward the posterior styles, anterior and anterior-lateral glands 1.4–1.5 mm long, ca 1.4 mm wide, posterior-lateral glands ca 1.2 mm long, ca 1 mm wide, all glands with the apex and abaxial face smooth. Anterior style ca 5.2 mm long, ca 0.4 mm wide, the distal ⅓ slightly inclined toward the posterior petal, posterior styles 5.4–5.5 mm long, ca 0.3 mm wide, divergent, the distal ⅓ arced toward the posterior-lateral petals, all styles with scattered hairs in the proximal ½–¾ of their lengths, stigmas ca 0.5 mm in diameter, capitate. Samara not seen.

Type. *Anderson et al. 36870.* Brazil. Bahia: Espigão Mestre, ca 100 km WSW of Barreiras, 750–800 m, 8 Mar 1972 (holotype UB, isotype NY).

Peixotoa megalantha is known only from the type (Fig. 7). It is a coarse, low shrub which is characterized by being larger in nearly all its parts than other species. The persistent stem and inflorescence stipules are 16–23 mm long. The orbicular limbs of the lateral petals are ca 16 mm in diameter. Such large flowers are found in only three other species. *P. hispidula,* which grows along the coast from Bahia to São Paulo, has petiolate inflorescence leaves; those of *P. megalantha* are sessile. *P. magnifica* of Goiás, Mato Grosso and eastern Bolivia has styles 7–9.2 mm long; the anterior style bears an oblong stigma at the apex but laterally on the abaxial surface. The styles of *P. megalantha* are less than 6 mm long and all bear capitate stigmas. In *P. reticulata,* an apomict with usually closed anthers containing mostly aborted pollen, the more distal inflorescence stipules are less than 15 mm long, deciduous, and smaller than the stem stipules. *P. reticulata* has not been reported from Bahia.

21. Peixotoa octoflora C. Anderson, sp. nov. Fig. 21.

Suffrutex usque ad 2 m. Stipulae vegetativae deciduae, ignotae, inflorescentiae 7.5–8.2 mm longae, acutae, deciduae. Petioli 10–17 mm longi. Laminae 7.8–11.6 cm longae, 6.6–10.4 cm latae, ovatae vel suborbiculares, supra velutinae, subtus ferentes pilos T-formes interdum laxe tomentosae, basi justa costam biglandulosae. Folia inflorescentiae petiolo brevi, distaliora linearia, supra glabra, subtus dense velutina. Inflorescentia terminalis, umbellis singularibus, 8-floribus; pedicelli 13–26 mm longi, 4 sessiles, 4 pedunculati, pedunculis 1–2.5 mm longis. Bracteae bracteolaeque praesentes. Sepala 7.2–7.8 mm longa. Limbus petalorum lateralium 14.5–15.2 mm longus, orbicularis, margine glanduloso-fimbriato, interdum eglanduloso. Limbus petali postici 10–12 mm longus, orbicularis, margine ¾ proximalibus glandulis capitatis ornato, ¼ distali glanduloso-fimbriato. Filamenta staminum subaequalia. Filamenta staminodiorum anticorum subaequalia postica superantia. Styli subaequales, 4.8–5.3 mm longi, anticus erectus vel parum inclinatus versus petalum posticum, postici divergentes, arcuati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Subshrub to 2 m. Vegetative branches golden tomentulose-velutinous. Stem stipules deciduous, not seen; inflorescence stipules 7.5–8.2 mm long, 8.6–10 mm wide, cordate, apex acute, adaxially the proximal ¼ densely velutinous, the distal ¾ glabrous, abaxially densely velutinous, deciduous. Stem leaves with the petiole 10–17 mm long, densely golden velutinous, laminas 7.8–11.6 cm long, 6.6–10.4 cm wide, ovate or suborbicular, apex apiculate, base cordate, velutinous above, pubescent with T-shaped hairs or sometimes loosely tomentose below, a pair of sessile glands halfway on the petiole, or sometimes at the base at the costa, each gland 1.2–1.4 mm in diameter. Inflorescence leaves with the petiole at least 2 mm long, laminas abruptly smaller than the cauline, the smallest not less than 2.8 mm long, ca 1 mm wide, the more proximal shaped like the cauline but more densely pubescent, the more distal linear, apex acuminate, glabrous above, densely velutinous below, a pair of glands at the base at the costa or halfway on the petiole, each gland 1–1.7 mm in diameter. Inflorescence terminal, the axes densely velutinous, internodes of the primary axis 3.1–7.5 cm long, 2° axes 2.4–14.7 cm long, 3° axes 2.1–5.5 cm long, subsidiary axes absent; umbels 8-flowered, of four pairs, in each pair one pedicel pedunculate, one pedicel sessile, primary peduncles 1–2.5 mm long, secondary peduncles absent. Bracts 0.6–1.2 mm long, 0.8–1 mm wide, triangular, glabrous adaxially, tomentulose abaxially; bracteoles 0.4–0.5 mm long, 0.3–0.5 mm wide, oblong, glabrous adaxially, glabrous or sparsely tomentulose abaxially. Pedicels 13–26 mm long, densely velutinous. Sepals 7.2–7.8 mm long, 0.6–0.8 mm wide, adaxially the proximal ½ glabrous, the distal ½ tomentulose, glands 1.3–1.7 mm long, 0.9–1.2 mm wide. Claw of the lateral petals 3.2–3.5 mm long, limb 14.5–15.2 mm long, 14–15 mm wide, orbicular, base briefly attenuate, fimbriae up to 1 mm long, glandular or sometimes eglandular. Claw of the posterior petal 5.5–6 mm long, limb 10–12 mm long, 10–11 mm wide, orbicular, fimbriae up to 1 mm long, those of the proximal ¾ capitate-glandular, the distal ¼ fimbriate-glandular. Lateral stamen filaments 5–6 mm long, posterior filament 4.8–5 mm long, usually a little shorter than the lateral four, arced toward the posterior petal, anthers 1.6–1.7 mm long, glandular connectives 0.7–0.8 mm long. Pollen grains 57–70 μm. Filament of the anterior staminode 5.5–6 mm long, anterior-lateral filaments 5–5.5 mm long, equal to or a little shorter than the anterior filament, posterior-lateral filaments 4.2–4.5 (–5) mm long, inflexed between the posterior styles, anterior and anterior-lateral glands 1.4–1.5 mm long, ca 1.3 mm wide, posterior-lateral glands ca 1.1 mm long, ca 0.9 mm wide, all glands with the apex and abaxial face smooth. Styles 4.8–5.3 mm long, 0.4–0.5 mm wide, anterior style usually a little stouter

than the posterior two, erect or slightly inclined toward the posterior petal, posterior styles divergent, arced toward the posterior-lateral petals, all styles glabrous or with a few scattered hairs near the base, stigmas 0.4–0.6 mm in diameter, capitate. Samara not seen.

Type. *Irwin et al. 16681a*. Brazil. Mato Grosso: Serra do Roncador, ca 60 km N of Xavantina, 550 m, 6 Jun 1966 (holotype UB, isotypes MICH, NY).

Peixotoa octoflora is known only form the type (Fig. 8). It is the only species in the genus which bears 8-flowered umbels. Each umbel consists of four pairs of flowers. Each pair has the pedicel of one flower sessile, the other pedicel on a short (1–2.5 mm long) primary peduncle. The type is apparently an apomict. The closed anthers contain pollen that is mostly aborted and 95% non-staining in cotton blue in lactophenol.

22. Peixotoa paludosa Turczaninow, Bull. Soc. Nat. Moscow **31**(1): 393. 1858. Fig. 15.

P. parviflora var. β *primaeva* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 34. 1912. Type. *Glaziou 13598*, pro parte (holotype B, destroyed, isotypes, C! K!).

Vine over 5 m long. Vegetative branches velutinous or tomentulose, pubescence abraded from older parts. Stem stipules ca 10 mm long, ca 9 mm wide, triangular, apex acute, finely velutinous adaxially, velutinous or tomentulose-velutinous abaxially, deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 2.5 mm long, 3 mm wide, densely velutinous in the proximal ¼ and sparsely so or glabrate in the distal ¾ adaxially, tomentulose-velutinous abaxially, very densely white tomentulose along the margins, persistent or eventually deciduous. Stem leaves with the petiole (4–) 5–17 mm long, densely velutinous or densely tomentose, laminas 4.8–14.3 cm long, 3–9.2 cm wide, elliptical or broadly elliptical or obovate, apex apiculate, base slightly cordate or almost truncate, velutinous or densely so above, loosely, sometimes sparsely, pubescent with T-shaped hairs or tomentose below, a pair of sessile glands borne on the surface of the blade 3–29 mm above the base, 1.5–17 mm from the costa, each gland 0.4–1.2 mm in diameter, or one or both glands absent. Inflorescence leaves with the petiole 1.2 mm or more long, laminas abruptly smaller than the cauline or gradually decreasing in size toward the distal nodes, the smallest not less than 1.8 mm long, 0.5 mm wide, shape of the more proximal like the cauline, the more distal narrowly lanceolate or linear, apex acuminate and sometimes with a tiny gland, sparsely velutinous or glabrous adaxially, densely velutinous or sericeous-velutinous abaxially, a pair of glands near or at the base or at the costa or sometimes halfway on the petiole, each gland 0.3–0.8 mm in diameter, rarely the larger laminas with a second pair near the base; rarely the most distal leaves reduced to sessile, linear or subulate, eglandular bracts, 0.7–4 mm long, 0.3–1.6 m wide. Inflorescence terminal or axillary, the axes velutinous or velutinous-tomentulose, internodes of the primary axes 2.3–10 cm long, 2° axes 0.7–12.5 cm long, 2° subsidiary axes 0.9–8 cm long, 3° axes 0.5–6.2 cm long, 3° subsidiary axes 0.5–20 mm long, 4° axes 0.4–12 mm long; umbels 4-flowered, one umbel per node, primary peduncles absent, secondary peduncles rare, up to 0.1 mm long. Bracts 0.2–0.4 (–1.2) mm long, 0.3–0.9 (–1.2) mm wide, triangular or semicircular, glabrous, sometimes tomentulose on the margins; bracteoles 0.1 mm long and wide, triangular, glabrous; sometimes bracts and bracteoles absent. Pedicels 11–19 mm long, velutinous or velutinous-tomentulose, often a little longer in fruit. Sepals 3.2–4.8 mm long, 1.8–2.5 mm wide, adaxially finely velutinous, or the proximal ⅔ glabrous, the distal ⅓ velutinous, glands 1.4–2.4 mm long, 0.7–1.3 mm wide.

Claw of the lateral petals 2–2.7 mm long, limb 9–11.5 mm long, 9.3–10 mm wide, broadly obovate or broadly elliptical or suborbicular, base briefly attenuate, fimbriae up to 0.9 mm long, usually glandular, sometimes a few eglandular. Claw of the posterior petal 3.3–4 mm long, limb 5.3–7 mm long, 5–6.3 mm wide, obovate, fimbriae up to 1 mm long, capitate-glandular, or sometimes the proximal ½ capitate-glandular, the distal ½ fimbriate-glandular. Stamen filaments 3.6–4.5 mm long, posterior filament equal to or shorter than the lateral four, strongly arced toward the posterior petal, anthers 1.1–1.4 mm long, glandular connectives 0.6–0.7 mm long. Pollen grains ca 50 μm. Anterior staminode filament 3.7–4.3 mm long, always exceeding the lateral four, anterior-lateral and posterior-lateral filaments 3.5–4.1 mm long, posterior-lateral filaments strongly inflexed between the posterior styles, anterior gland 1.4–1.6 mm long, 1.3–1.5 mm wide, anterior-lateral and posterior-lateral glands 1.1–1.4 mm long, anterior-lateral glands 1.1–1.4 mm wide, posterior-lateral glands 0.8–1.3 mm wide, usually narrower than the anterior-lateral two, all glands with the apex and abaxial face smooth. Styles 4–5.5 mm long, 0.3–0.4 mm wide, the anterior style sometimes a little longer and usually a little stouter than the posterior two, strongly arced toward the posterior petal, posterior styles strongly divergent, inclined toward the posterior-lateral petals, stigmas 0.3–0.5 mm in diameter, capitate. Carpophore up to 3 mm long. Torus up to ca 3.5 mm high. Samara with the dorsal wing 2.8–3.1 cm long, 1.5–1.7 cm wide, upper margin arced or straight, lower margin arced or slightly so, erose, lateral wings 6–8.5 mm wide, 12–14 mm high, rectangular or semicircular, entire, erose, or irregularly dentate, areole 3.2–3.5 mm long, 2.7–3.5 mm wide, nut ca 4.5 mm long, 3.5–4 mm in diameter, mature seeds not seen.

Type. *Blanchet 2867*. Brazil. Bahia: ". . . in paludibus d'Ilhabira [Itabira], prope urbem di Barro." (holotype CW?, isotypes BM! BR! F! G! K! LE! NY! P! W!).

Distribution. (Fig. 7). North-central Minas Gerais, especially the Serro do Espinhaço, and Bahia; cerrado, campo sujo, caatinga, and at forest margins.

BRAZIL. Bahia: type q.v.; ca 35 km N of Bom Jesus da Lapa, on main road to Ibotirama, ca 450 m, 43°19′W, 12°58′S, *Harley et al. 21561* (MICH); Chapadão Ocidental da Bahia, 37 km SE of Correntina, on road to Jaborandí, ca 600 m, ca 44°28′W, 13°35′S, *Harley et al. 21964* (MICH). Minas Gerais: 22 km by road W of Januária on road to Serra das Araras, 610 m, *Anderson 9197* (MICH, NY); Belo Horizonte, *Barreto 7545* (UB), *8681* (R); *Claussen 68A* (BR, F, W); mun. Santa Luzia, Lagôa Santa, *da Costa s.n.* (R 72044); entre Diamantina, Mendanha e Morro do Ramão, *Glaziou 13598 p.p.* (C, K, type of *P. parviflora* var. *primaeva*); entre Taquaruçú e Serrinha, *Glaziou 18929 p.p.* (C, K, LE, R); mun. Caimópolis, rod. Fernão Dias, *Hatschbach 41427* (MICH); Serra do Taquaril, Nova Lima, *Roth 1587* (RB); *Warming 238* (C); Contagem, Rio Paraopeba, *Warming s.n.* (C); *Warming s.n.* (C, GOET, P, US); mun. Belo Horizonte, Morro das Pedras, *Williams & Assis 6490* (GH); mun. Belo Horizonte, Colonia Afonsa Pena, *Williams & Assis 7231* (GH).

In *P. paludosa* the leaf glands are borne on the surface of the lamina away from the base and costa. Within the range of *P. paludosa* only *P. spinensis* also bears the glands in this manner. It differs in that its leaves are densely tomentose to woolly below, and in that the anterior and anterior-lateral staminode glands have an indentation across the apex and decurrent on the abaxial face. The leaves of *P. paludosa* are more moderately pubescent, and the staminode glands are smooth. Also, the flowers of *P. paludosa* are slightly smaller than those of *P. spinensis*. In *P. leptoclada*, of Minas Gerais and Goiás, the larger leaves sometimes bear the glands on the surface away from the base and costa. This species, which may be a close relative, has similar but larger flowers, but differs most strikingly in its large stipules. Those of the stem are ca 11–20 mm long and wide and are usually persistent. Those of the inflorescence are at least 7 mm long and are persistent at the more distal nodes. In *P. paludosa* the stem stipules are ca 9–10 mm long and wide, and deciduous. Those of the inflorescence are usually less

than 7 mm long and wide (only rarely more), and, while persistent for a while, are eventually deciduous.

Roth 1587 is unusual in that the specimens are apparently apomictic. The anthers are closed and contain aborted pollen that is 99% non-staining in cotton blue in lactophenol.

The type locality is unknown. According to Urban (1895), during the years 1833–1847 Blanchet sent an assistant on collecting trips along the southern coast of Bahia and as far inland as the Rio São Francisco. Many of the exact localities for the collections made during these expeditions have not been ascertained. Only two additional collections of *P. paludosa* are known from Bahia. These were made by Harley in 1980. The specific epithet is doubtlessly a misnomer. *P. paludosa* has never been collected in wet areas. More likely the type was found in a dry area near the "marais d'Itabira."

Niedenzu (1912) described *P. parviflora* var. *primaeva* based on *Glaziou 13598*. He considered this variety an ancestral type, because in his material the staminodes had tiny locules ("Androecium fere *Banisteriae* sectionis *Pachyzeugmatis*. . ."). However, *Glaziou 13598* is a mixed collection of *P. paludosa* and of *Banisteriopsis malifolia* (Nees & Martius) Gates var. *malifolia*. The photograph of the holotype (at B, now destroyed) shows a specimen of *P. paludosa* in bud. The isotypes at C and K are also in bud, but flowers of *B. malifolia* are contained in the packets mounted with the specimens. Niedenzu doubtlessly based his description on such flowers supplied with the Berlin specimen.

Collected in flower from January through September, in fruit from April through August.

23. Peixotoa parviflora Adr. Jussieu in St. Hilaire, Fl. Bras. Mer. **3**: 62. 1832 [1833]. Figs. 2, 18.

P. discolor Grisebach, Linnaea 13: 216. 1839. Type. *Sellow s.n.* [*Sellow III. it. c1313* (28 May 1819), fide Niedenzu, 1912] (holotype, B destroyed, isotype K!).

Scandent shrub or vine to 3 m. Vegetative branches finely or loosely, often golden, velutinous, pubescence abraded from older parts. Stem stipules 5.5–17 mm long, 5–17 mm wide, cordate, apex acute, velutinous or tomentulose adaxially, velutinous-sericeous or velutinous-tomentulose abaxially, deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 3 mm long, 4 mm wide, entire with the apex acute or notched, or rarely bifid, finely velutinous or tomentulose adaxially, sericeous-velutinous or tomentulose-velutinous abaxially, deciduous or persistent. Stem leaves with the petiole 4–32 mm long, (often golden) velutinous or velutinous-tomentulose, lamina 5.5–17.5 cm long, 3–10.6 cm wide, ovate or elliptical, sometimes obovate or orbicular, apex apiculate, base cordate or slightly so or rarely truncate, velutinous to densely so above, loosely pubescent with T-shaped hairs or loosely tomentose below, with a pair of sessile glands at the base at the costa or halfway on the petiole or rarely on the petiole just below the lamina or rarely on the lamina up to 1 mm above the base at the costa, each gland 0.7–2.3 (–4.3) mm in diameter, rarely one or both glands absent. Inflorescence leaves with the petiole (0.6–) 1 mm or more long, laminas usually abruptly smaller than the cauline, sometimes gradually decreasing in size toward the distal nodes, the smallest not less than 3 mm long, 0.6 mm wide, shape of the more proximal like the cauline, the more distal narrowly elliptical or lanceolate or oblanceolate or linear, apex acuminate or sometimes caudate, velutinous or sparsely so above, sericeous or sericeous-velutinous below, a pair of glands at the base at the costa or half-way on the petiole or rarely on the petiole just below the lamina, each gland (0.2–) 0.3–1.5 mm in diameter, rarely with a second, smaller pair (ca

0.4 mm in diameter) borne just above the pair of larger glands; rarely some of the inflorescence leaves reduced to sessile, linear, eglandular bracts, 2.5–3.5 mm long, ca 0.5 mm wide. Inflorescence terminal, the axes velutinous or velutinous-tomentulose, internodes of the primary axis 1–8.3 cm long, 2° axes 0.9–12.5 cm long, 2° subsidiary axes 0.8–4.2 cm long, 3° axes 1–10.8 cm long, 3° subsidiary axes 0.7–2.2 cm long, mature 4° axes not seen, usually at the more distal nodes the 2° and 3° axes suppressed, with 1 or 2 umbels borne on secondary peduncles in the leaf axil, very rarely subsessile, always with 3 umbels at the terminal nodes, each umbel 4-flowered, primary peduncles absent, secondary peduncles 0.5–17 mm long. Bracts 0.3–2.2 (–3) mm long, 0.3–1 mm wide, triangular or linear or rarely semicircular, glabrous or the margin velutinous or tomentulose; bracteoles 0.1–0.7 mm long, 0.1–0.5 mm wide, triangular or linear or oblong, glabrous or the margin velutinous or tomentulose. Pedicels 7–19 mm long, velutinous or sometimes velutinous-tomentulose, often a little longer in fruit. Sepals 2.2–4.7 mm long, 1.2–2 mm wide, adaxially glabrous or with the apex tomentulose or the proximal ⅓–½ glabrous, the distal ⅔–½ tomentulose, glands 0.7–2 mm long, 0.4–1.1 mm wide. Claw of the lateral petals 1.5–2.2 mm long, limb (4.3–) 5.2–9.5 mm long, (4–) 5–8.5 mm wide, orbicular or broadly obovate, base briefly attenuate, fimbriae up to 0.5 mm long, usually glandular, sometimes a few eglandular. Claw of the posterior petal (2.2–) 2.7–4 mm long, limb 3.5–6 (–6.8) mm long, 3–6.2 mm wide, obovate or broadly so or suborbicular, fimbriae up to 0.5 mm long, capitate-glandular or sometimes the apex fimbriate-glandular. Lateral stamen filaments 2.2–4 mm long, always exceeding the posterior filament, posterior filament (1.9–) 2.1–3 mm long, arced toward the posterior petal, anthers 0.8–1 mm long, glandular connectives 0.6–0.7 mm long. Pollen grain ca 42 μm. Anterior staminode filament 2.1–3.3 (–4) mm long, always exceeding the lateral 4, lateral staminode filaments 1.8–3.2 (–3.8) mm long, the anterior-lateral filaments usually longer, sometimes shorter, than the posterior-lateral two, or sometimes the four lateral filaments subequal, posterior-lateral filaments inflexed or only slightly so between the posterior styles, anterior and anterior-lateral glands (1–) 1.1–1.5 mm long, 1.3–1.4 mm wide, posterior-lateral glands 0.8–1.2 mm long, 0.9–1 mm wide, usually a little shorter but always narrower than the anterior three, all with the apex and abaxial face smooth. Styles 2.3–3.7 mm long, 0.3–0.4 mm wide, the anterior style often a little longer, sometimes a little shorter, than the posterior two, anterior style arced toward the posterior petal, posterior styles divergent, arced (not as strongly as the anterior style) toward the anterior-lateral petals, all styles usually with scattered hairs in the proximal ½ of their lengths, stigmas 0.3–0.4 mm in diameter, capitate. Carpophore up to 0.5 mm long. Torus up to 3.5 mm high. Samara with dorsal wing 1.6–1.9 cm long, 0.8–0.9 cm wide, upper margin straight or gently sigmoid, lower margin arced or slightly sigmoid, entire or slightly erose, lateral wings 2.5–3.6 mm wide, 6.7–8.8 mm high, rectangular or semicircular, slightly erose to sometimes dentate, areole 3–3.3 mm long, 3–3.5 mm wide, nut 4.5–5 mm long, 2.8–3.5 mm in diameter, seed ca 6 mm long, outer cotyledon ca 6.5 mm long, ca 2.5 mm wide, folded at ca ½ of its length, inner cotyledon ca 4.2 mm long, ca 2.2 mm wide, folded at ca ⅓ of its length.

Type. *St. Hilaire s.n.* Brazil. Minas Gerais: ". . . in pascuis juxta Conceáo [Conceição] . . ." (holotype P!, isotype P!).

Distribution. (Fig. 8). From central and southern Minas Gerais and Rio de Janeiro to eastern São Paulo and eastern Paraná; cerrado, campo, woodlands, and gallery forests.

BRAZIL. Minas Gerais: *Ackermann s.n.* (BR); Morro do Pilar, *Black & Magalhães 51-12228* (UB); Serra do Taquaral, Ouro Preto, *de Brito, Jr. s.n.* (SP 18835); 4 km W of Morro do Pilar, 20 km from road between Conceição and Belo Horizonte, *Gates 384* (MICH); Serra de Biribiri, 7 km W of Diamantina, 1200 m, *Glassman & Gomes, Jr. 8119* (SP); Taquaruçú á Serrinha, *Glaziou 18929 p.p.* (P);

FIG. 8. Distribution of *P. octoflora* and *P. parviflora*.

Diamantina á Tombador, *Glaziou 18930* (C, P, R); Presidente Soares, *Heringer 10295* (UB); Santa Bárbara, *Hoehne s.n.* (SP 5052); Serro Frio, *Martius s.n.* (M); Serra dos Pinheiros, *Pohl 3556 (d. 1557)* (K, W); Caldas, *Regnell-III 118* (US), *III-318* (F, P, S, US); *III-318x* (S), *III-1652* (F, S, US, W); Santa Luzia, *Riedel & Luschnath I* (LE, S); Serra do Taquaral, Ouro Preto, *Silva Novaes s.n.* (SP 18839); Ouro Preto, *Texeira s.n* (SP 18826); Caldas, *Widgren* in 1845 (BR, F, K, LE, S, US); *Williams & Assis 6619* (GH). Paraná: 2 km W of intersection of PR-11 and the Rio Itarare at the border of Paraná and São Paulo, 620 m, *Davidse et al. 11371* (MO); Sengés, *Dusén 9942* (GH, S); Jaguariahyva [Jaguariaíva], 740 m, *Dusén 340a* (GH, MO, S), *9225* (A, BM, F, G, GH, K, MO, NY, S, US), *9619* (S), *9690* (F, S), *11685* (A, BM, G, GH, K, MO, NY, S, US), *13032* (S), *13082* (S); mun. Tibagi, Balsa para Piraí, 696 m, *Hatschbach 6028* (US), mun. Tibagi, Fazenda Monte Alegre, Harmonia, *Hatschbach 2831* MICH, RB); mun. Sengés, Fazenda Morungava, Rio do Funil, *Hatschbach 5347* (MICH, US); Jaguariaíva, *Hoehne s.n.* (SP 23414); 4 km N of Wenceslau Braz, *Lindeman & Haas 3131* (K, MBM, NY); Tibagi, *Reiss 65a* (F); mun. Sengés, Fazenda Morungava, Rio Funil, ca 24°08′S, 49°22′W, 800 m, *Smith et al. 14834* (US). Rio de Janeiro: Rio de Janeiro, *Ackermann 232* (P-JUSS), *Ackermann s.n.* (BR), *Burchell A882* (K); Petrópolis á Santo Antonio, *Glaziou 5785* (C, P), *8581* (C, P), *10371* (BR, C, G, K, LE, P, US); pr. Sumidero, na rodovia BR-3 entre Itaipava e Pedro do Rio, ca 600 m, *Pabst 10321* (RB); Serra dos Órgãos, *Riedel III* (LE, S); *Sellow I. it. [a 1814]* (K?, NY); Petrópolis, mata do Judio, ca 700 m, *Sucre 7560* (MICH); mun. Araras, 850–980 m, *Sucre 10614* (MICH). São Paulo: Jaraguá, *Brade 5949* (S, SP); Campinas, *Campo Novaes 651* (SP, US); Cotia, *Constantino s.n.* (RB 45430); Jaraguá, *Hoehne s.n.* (SP 5479); estrada de Pirapóra á Cabreúva, *Hoehne s.n.* (F, GH, NY, SP 12905); São Paulo, 800 m, *Holway & Holway 1496* (US); Amparo, *Kuhlmann 1192* (SP); Igaratá, *Kuhlmann 2758* (SP); ca 10 km SW de Jundaí. Serra do Japí, *Leitão Filho et al. 3164* (NY, US); *Löfgren 272* (C); mun. Itapeva, Itanguá, ca 1000 m, *Vidal s.n.* (R 72157, R 72400); Sorocaba, *Wacket s.n.* (W); circa Parnahyba [Parnaiba] ad fl. Tieté, ca 700 m, *Wettstein & Schiffner s.n.* (W).

Peixotoa parviflora is readily recognized by its inflorescence structure. The terminal nodes bear three umbels and thus are 12-flowered. The lateral umbels and often also the terminal umbels are borne on secondary peduncles. Commonly at the more distal nodes the secondary and tertiary axes are suppressed and one or two umbels are borne on secondary peduncles in each leaf axil. The inflorescence leaves are always petiolate. The flowers are unusual in that the posterior styles are curved toward the anterior-lateral petals instead of toward the posterior-lateral petals. Only three other species share the inflorescence

structure but not the curvature of the styles. *P. adenopoda* from east-central Bahia has stalked leaf glands and staminode glands that have an indentation across the apex and decurrent on the abaxial face. *P. catarinensis* from coastal Santa Catarina has tiny leaf glands (0.2–0.7 mm in diameter) which are borne on the surface of the lamina away from the base and costa. In *P. parviflora* the staminode glands are smooth. The leaf glands are sessile and borne at the base at the costa or halfway on the petiole or rarely entirely on the petiole just below the lamina. They are 0.7–2.3 (–4.3) mm in diameter. *P. tomentosa* is probably closely related and the species most likely to be confused with *P. parviflora*. Its range, the central region of the Serra do Espinhaço of Minas Gerais, falls within that of *P. parviflora*. Its flowers are larger than those of *P. parviflora*. Sessile inflorescence leaves and sessile umbels at the more distal nodes are common. The pubescence of the inflorescence axes and of the lower leaf surface also usually help to separate the two species. The young branches and inflorescence axes of *P. tomentosa* are very densely golden velutinous. In *P. parviflora* the hairs are commonly white and only sparsely to moderately abundant. The leaves of *P. tomentosa* are usually densely tomentose or woolly below while those of *P. parviflora* are sparsely to moderately pubescent with T-shaped hairs or moderately tomentose but never woolly below.

One of the few species that have a relatively wide range, *P. parviflora* shows some geographical variation in flower size. Specimens from Rio de Janeiro tend to have the smallest flowers, those from Paraná the largest.

Collected in flower throughout the year, in fruit in January, June, July, and August.

24. Peixotoa psilophylla C. Anderson, sp. nov. Fig. 21.

Suffrutex usque ad 2 m. Stipulae vegetativae 8.6–15 mm longae, acutae vel bifidae, interdum persistentes. Petioli 3.3–6.5(–8.8) mm longi. Laminae (3.7–) 6.3–20.7 cm longae, (3.6–)5–9.5 cm latae, rugosae, ellipticae vel ovatae vel lanceolatae, supra glabrae vel sparsim velutinae, subtus glabrae vel in venis sparsim velutinae, basi juxta costam biglandulosae. Folia inflorescentiae petiolo brevi vel seśsilia, distaliora lineari-lanceolata vel subulata. Inflorescentia terminalis vel axillaris, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 16–34 mm longi. Sepala 4.5–6.5(–7) mm longa. Limbus petalorum lateralium 11.5–15 mm longus, orbicularis, margine denticulato, glanduloso vel eglanduloso. Limbus petali postici 8.5–9 mm longus, late obovatus, margine ⅔–¾ proximalibus glandulis capitatis ornato, ⅓–¼ distali denticulato, glanduloso vel eglanduloso. Filamenta staminum subaequalis. Glandulae 3 staminodiorum anticorum apice non profunde indentatae, plerumque indentatione in pagina abaxiali decurrenti. Stylus anticus 3.2–4 mm longus, saltem parum inclinatus versus petalum posticum, styli postici 3.4–4.3 mm longi, interdum inaequales, divergentes, arcuati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Subshrub to 2 m. Vegetative branches purplish-brown, sparsely tomentulose when young, older parts glabrous. Stem stipules 8.6–12 mm long, 9–15 mm wide, cordate or triangular-cordate, entire with the apex acute or notched, or bifid, finely tomentulose or velutinous adaxially, velutinous-tomentulose abaxially, deciduous, sometimes persistent; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 6.3 mm long, 6.2 mm wide, entire with the apex acute or sometimes notched, more densely pubescent than the cauline, eventually deciduous. Stem leaves with the petiole 3.3–6.5 (–8.8) mm long, tomentulose-velutinous or sparsely so, sometimes glabrous, laminas (3.7–) 6.3–20.7 cm long, (3.6–) 5–9.5 cm wide, elliptical or ovate or lanceolate, apex apiculate, base cordate, rugose, glabrous or sparsely

velutinous above, especially along the veins, glabrous or with scattered hairs on the major veins below, especially near the base, a pair of sessile glands at or up to 0.7 mm above the base at the costa or halfway on the petiole, each gland 1–2.1 mm in diameter. Inflorescence leaves petiolate or sometimes sessile at the distal nodes, laminas abruptly smaller than the cauline, linear-lanceolate to linear to subulate, the smallest not less than 3 mm long, 0.6 mm wide, apex acuminate, tomentulose-velutinous above, densely velutinous below, a pair of glands at the base at the costa or halfway on the petiole, each gland 0.8–1.6 mm in diameter, sometimes with a second, smaller pair (0.5–0.6 mm in diameter) below the larger pair, rarely one or both glands absent. Inflorescence terminal or axillary, the axes velutinous-tomentulose, internodes of the primary axis 2.7–15 cm long, 2° axes 2.8–11.1 cm long, 2° subsidiary axes 1.8–2.7 cm long, 3° axes 0.9–3.3 cm long; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.4–1.3 mm long, 0.5–1 mm wide, triangular, glabrous or tomentulose, or tomentulose only abaxially and/or on the margins; bracteoles 0.2–0.5 mm long, 0.2–0.4 mm wide, triangular, sometimes linear or semicircular, glabrous or tomentulose, or sometimes tomentulose only abaxially and/or on the margins. Pedicels 116–34 mm long, velutinous, Sepals 4.5–6.5 (–7) mm long, 2.3–2.7 (–3) mm wide, adaxially the proximal ⅓–½ glabrous, the distal ⅔–½ velutinous-tomentulose, glands 1.6–2.4 (–2.7) mm long, 0.8–1.2 mm wide. Claw of the lateral petals 2.3–2.6 mm long, limb 11.5–15 mm long, 11–14.5 mm wide, orbicular, base briefly attenuate, denticulate, teeth up to 0.6 mm long, glandular or eglandular. Claw of the posterior petal 4–4.5 mm long, limb 8.5–9 mm long, 8.5–10 mm wide, broadly obovate, margin of the proximal ⅔–¾ capitate-glandular, fimbriae up to 0.3 mm long, margin of the distal ¼–⅓ denticulate, teeth up to 0.1 mm long, glandular or eglandular. Lateral stamen filaments 3.5–4.1 mm long, posterior filament 3.3–3.7 mm long, always at least slightly shorter than the lateral four, slightly arced toward the posterior petal, anthers 1.4–1.5 mm long, glandular connectives 0.6–0.8 (–1) mm long. Pollen grains 50–57 μm. Filament of the anterior staminode 3.8–5 mm long, anterior-lateral filaments 3.6–4.5 mm long, posterior-lateral filaments 3.4–3.8 mm long, always shorter than the anterior three, inflexed between the posterior styles, anterior and anterior-lateral glands 1.3–1.4 mm long and wide, posterior-lateral gland 1.2–1.3 mm long, 1.1–1.2 mm wide, anterior and anterior-lateral glands usually with a shallow indentation across the apex and decurrent on the abaxial face, posterior-lateral glands smooth. Anterior style 3.2–4 mm long, ca 0.4 mm wide, slightly inclined toward the posterior petal, posterior styles 3.4–4.3 mm long, ca 0.3 mm wide, sometimes unequal, always exceeding the anterior style, divergent, arced toward the posterior-lateral petals, all styles usually glabrous, sometimes with scattered hairs in the proximal ⅓ of their lengths, stigma of the anterior style 0.4–0.5 mm in diameter, stigmas of the posterior styles 0.3–0.4 mm in diameter, all capitate. Samara not seen.

Type. *Irwin et al. 16860*. Brazil. Mato Grosso: Ca 15 km S of Xavantina, 400 m, 10 Jun 1966 (holotype UB, isotypes MICH, NY).

Distribution. (Fig. 10). Known only from the vicinity of Xavantina of east-central Mato Grosso; cerrado and margins of gallery forests.

BRAZIL. Mato Grosso: Xavantina, 400 m, *Irwin et al. 16778* (NY, UB); ca 70 km S of Xavantina, 500 m, *Irwin et al. 17439* (MICH, NY, UB); ca 3 km S of Xavantina, *Ratter R112 p.p.* (NY); Xavantina, *Richards 6429* (K, NY, P); Chavantina [Xavantina], *Sick B481* (RB).

Peixotoa psilophylla is the only species in Mato Grosso with the stem leaves glabrous or very sparsely pubescent when mature. The internodes of the primary inflorescence axis and the slender secondary axes are commonly 5–15 cm long, and give the inflorescence an open appearance. The hairs of the inflorescence and any other part of the plant are white. The anterior and anterior-

lateral staminode glands usually have an indentation across the apex and decurrent on the abaxial face. The margin of the limbs of the lateral petals and of the distal section of the limb of the posterior petal is denticulate. The geographically nearest glabrous species is *P. hatschbachii* of south-central Goiás, which is distinguished by its stalked leaf glands. In *P. psilopylla* the leaf glands are sessile. *P. hatschbachii* also differs in its smaller flowers whose petals are fimbriate, its larger stem stipules (over 17 mm long and wide), and its smooth staminode glands.

Collected in flower in June and July.

25. Peixotoa reticulata Grisebach, Linnaea **13**: 213. 1839. Figs. 22, 23.

P. macrophylla Grisebach, Linnaea 13: 214. 1839. Type. *Sellow s.n.* [*Sellow IV. it. 5505*, fide Niedenzu, 1912] (Lectotype NY!).

P. lateritia Adr. Jussieu, Ann. Sci. Nat. Sér. II, Bot. 13: 279. 1840. Type. *Claussen s.n.* (holotype P-JUSS!).

P. hirta f. 1. *minor* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 35. 1912. Type. *Warming s.n.* (23 Sep 1864) (lectotype C!, isotypes F! LE! US!).

P. hirta f. 2. *macrophylla* (Grisebach) Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 35. 1912.

P. macrophylla f. I. *minor* (Niedenzu) Niedenzu, Das Pflanzenreich IV. 141: 524. 1928.

P. macrophylla f. II. *typica* (Grisebach) Niedenzu, Das Pflanzenreich IV. 141: 524. 1928.

P. grandiflora Ferreira, An. Soc. Bot. Brazil, XX Cong. Nac. Bot. Goiana: 281. 1969. Type. *Ferreira 2b* (UB 37618) (holotype UB!).

Shrub or subshrub, sometimes scandent, to 3 m. Vegetative branches finely velutinous or tomentulose, older parts usually glabrate. Stem stipules 8–25 mm long, 9.6–25 mm wide, entire with the apex acute, or bifid, velutinous or tomentulose or glabrate adaxially, tomentose-velutinous or sericeous-velutinous abaxially, deciduous; inflorescence stipules gradually decreasing in size toward the distal nodes, the smallest not less than 5.5 mm long and wide, entire with apex acute or notched, or bifid, sometimes the most distal fused at the base, deciduous. Stem leaves with the petiole 3–14 (–15.5) mm long, (sometimes golden) tomentose or velutinous-tomentose, laminas 3.5–17.5 cm long, 2.2–12 cm wide, elliptical, ovate, suborbicular, rarely lanceolate, the smaller sometimes obovate or rhombic, apex apiculate, base cordate or sometimes truncate, rugose, velutinous above, loosely pubescent with T-shaped hairs or loosely tomentose or tomentulose below, rarely the pubescence restricted to the major veins below, a pair of sessile glands at the base at the costa or, more commonly, halfway on the petiole, rarely borne on the surface of the blade up to 1 mm above the base, up to 1.5 mm from the costa, each gland (0.7–) 1–2.2 (–3.2) mm in diameter, rarely with a second smaller pair (0.4–0.8 mm in diameter) immediately above the larger pair. Inflorescence leaves with the more proximal petiolate, usually the more distal sessile, laminas abruptly smaller than the cauline, the smallest not less than 1.4 mm long, 0.6 mm wide, shape of the more proximal like the cauline, the more distal lanceolate or oblanceolate or linear, the most distal usually subulate, apex acuminate, sparsely velutinous or glabrous above, densely velutinous or velutinous-tomentose below, a pair of glands at the base or halfway on the petiole, each gland 0.3–2.3 mm in diameter, rarely with a second, smaller pair (0.6–1 mm in diameter) immediately above or adjacent to the larger pair, rarely one or both glands absent. Inflorescence terminal or axillary, the axes densely velutinous-tomentulose, internodes of the primary axis 1–12.5 cm long, 2° axes 0.7–11.8 (–15.2) cm long, 2° subsidiary axes rare, 2.5–3 cm long, 3° axes 0.5–6.5 cm long, 4° axes 0.4–3.8 cm long, 5° axes

1.1–3.5 cm long; umbels 4-flowered, one umbel per node, primary peduncles rare, up to 1.5 mm long, secondary peduncles up to 6 mm long or absent. Bracts 0.3–3.8 mm long, 0.2–1.3 (–2.3) mm wide, triangular or subulate, glabrous or velutinous or tomentulose or sparsely so on both surfaces or only abaxially or only on the margins; bracteoles 0.1–0.9 mm long, 0.1–0.6 mm wide, triangular or oblong or subulate, usually glabrous, sometimes tomentulose abaxially; bracts and bracteoles rarely absent. Pedicels 8–32 mm long, (sometimes golden) densely tomentulose-velutinous, usually at least slightly longer in fruit. Sepals 4–8.5 mm long, 2–4.3 mm wide, adaxially finely tomentulose or velutinous or pubescent with T-shaped hairs or sparsely so, or the proximal ¼–⅔ glabrous, the distal ¾–⅓ pubescent, glands 1.4–3 mm long, 0.7–1.5 mm wide. Claw of the lateral petals 2.2–2.5 (–3.5) mm long, limb (11.2–) 12–15 (–18) mm long, 12.5–15 (–18) mm wide, orbicular or broadly obovate, base briefly attenuate, fimbriae up to 1.2 mm long, glandular or eglandular. Claw of the posterior petal 3.5–5 mm long, limb 8–10 (–12) mm long, 7–10 (–12) mm wide, orbicular or broadly obovate or broadly elliptical, fimbriae up to 0.8 (–10) mm long, those of the proximal 1/2–4/5 capitate-glandular, the distal 1/2–1/5 fimbriate-glandular or sometimes all capitate-glandular. Filaments of the lateral stamens 3.5–4.7 (–5.3) mm long, posterior filament 3.3–4.7 mm long, usually shorter, sometimes subequal to the lateral four, slightly or strongly arced toward the posterior petals, anthers 1.3–1.7 mm long, glandular connectives 0.6–0.9 mm long. Pollen grains 57–63 (–70) μm. Filaments of the anterior and anterior-lateral staminodes 3.5–4.6 (–4.9) mm long, posterior-lateral filaments 3.2–4.3 mm long, usually a little shorter, sometimes equal to the anterior three, inflexed between the posterior styles, sometimes the anterior-lateral filaments exceeding the other three, glands 1.2–1.6 (–2) mm long, 1.1–1.5 mm wide, the posterior-lateral glands usually a little smaller than the anterior three, all glands with the apex and abaxial face smooth. Styles 3.6–5 mm long, 0.2–0.4 mm wide, equal or the anterior longer or shorter than the posterior two, the anterior style always a little stouter than the posterior two, anterior style arced or at least slightly inclined toward the posterior petal, posterior styles divergent along their entire length or only in the distal ⅓, arced toward the posterior-lateral petals, all styles usually glabrous, sometimes velutinous in the proximal ½ of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Samaras variable in size, the smaller usually with the dorsal wing 1.3–2 cm long, 0.9–1.3 cm wide, upper margin straight or gently sigmoid, lower margin arced or nearly so, erose or slightly so, lateral wings 1.3–2.5 mm wide, 6–8 mm high, rectangular, erose or sometimes lacerate, the larger samaras usually with the dorsal wing 2.3–4 cm long, 1.3–2.3 cm wide, upper margin straight, arced or sigmoid, lower margin sigmoid or slightly so or arced, lateral wings (2.7–) 3–7.5 mm wide, 9–15 mm high, rectangular or semicircular, erose or slightly so, all samaras with the areole 3.5–6.5 mm long, 3–6.8 mm wide, nut ca 4–6.5 (–7.5) mm long, 3–5.5 mm in diameter, seed 6.2–7.4 mm long, outer cotyledons 7.4–11.5 mm long, 1.5–2.2 mm wide, folded at ca ½–⅔ of its length, inner cotyledon 4.2–6 mm long, 1–2 mm wide, folded at ca 4/5–5/6 of its length or straight.

Type. *Sellow s.n.* [*Sellow III. it. c. 1310* (2. V 1819), fide Niedenzu, 1912] Brazil. Minas Gerais: ". . . pr. Juesshuy [Suaçui]." (lectotype NY!).

Distribution. (Fig. 9). From central Minas Gerais to Paraná, southern Goiás to central and southern Mato Grosso, eastern Paraguay and eastern Bolivia; cerrado and campo.

BOLIVIA. Prov. Velasco, *Kuntze s.n.* (NY). BRAZIL. Distrito Federal: Brasília, *Ferreira 3, 5, 7, 9, 13* (UB), *Heringer 8410* (UB, US), *11670, 11811* (UB), *Irwin et al. 11103* (MICH, NY), *Irwin & Soderstrom 5067* (MICH, NY), *6117* (MICH), *Martin 407* (GH), *Pires et al. 9086* (UB, US), *Sucre 274* (NY, RB, UB); Braslândia, *Ferreira 4* (UB); Lagôa Paranoá, 1000 m, *Irwin et al. 15340, 26641* (MICH, NY); Braslândia, *Lima et al. 1* (NY, UB); entre Brasília e Fercal, *Pires 58097* (MICH, NY). Goiás:

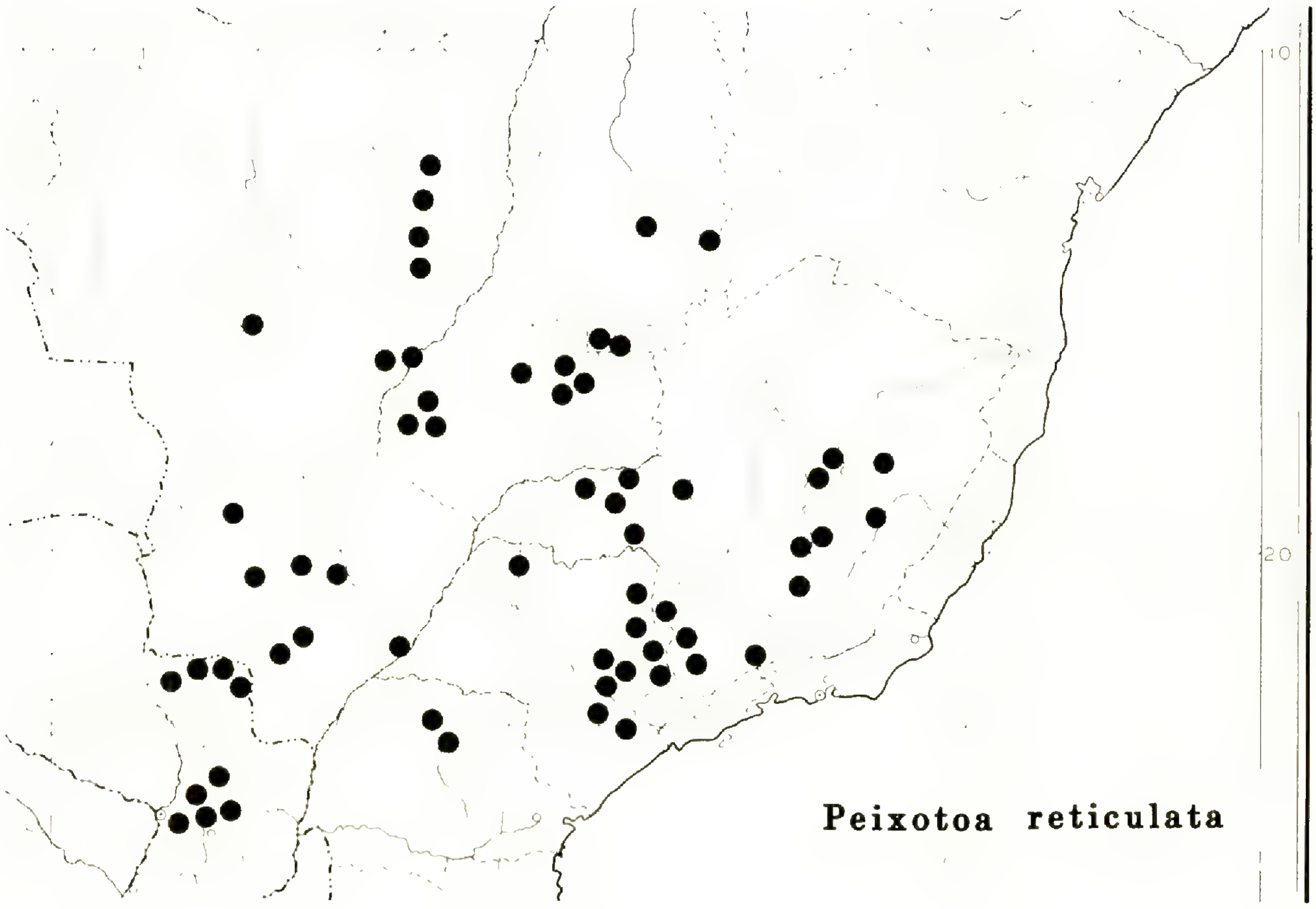

FIG. 9. Distribution of *P. reticulata*.

Serra do Caiapó, ca 25–30 km S of Caiapônia, 800–1200 m, *Anderson 9391, 9589* (MICH, NY); Serra dos Pirineus, ca 15 km N of Corumbá de Goiás, 1250–1300 m, *Anderson 10260* (MICH, NY); Goiás, *Burchell 7037* (K); Cavalcante, *Burchell 7596* (K); Chapada dos Veadeiros, Pouso Alto, 1800 m, *Ferreira 12* (UB); Goiânia, *Guimarães et al. 292* (MICH, RB); mun. Mineiros, BR-60, *Hatschbach 34639* (MICH); mun. Luzânia, *Heringer 14691* (UB); Rio da Prata, ca 6 km S of Posse, 14°S, 46°W, *Irwin et al. 14340a* (NY); Serra do Caiapó, ca 50 km S of Caiapônia, 1000 m, *Irwin et al. 17830* (MICH); Serra dos Pirineus, 20 km N of Corumbá de Goiás on road to Niquelândia, ca 1150 m, *Irwin et al. 18762* (NY); Serra dos Pirineus, ca 18 km E of Pirenópolis, 1000 m, *Irwin et al. 34248* (MICH, NY); Pirenópolis, cachoeira do Abade, *Onishi et al. 74* (UB); ad S. Pedro, *Pohl 472-2598(1498d)* (K, W). Mato Grosso: ca 5 km N of Barra do Garças, 500 m, *Anderson 9871* (MICH, NY); Campo Grande, *Archer & Gehrt 140* (SP, US); General Caneiro, *Hartmann 113* (SP); Rio Brilhante, *Hatchbach & Guimarães 21770* (C, M, MICH, P); Terenos, *Hatschbach 24625* (MBM, MICH); Casa da Pedra, *Hoehne s.n.* (SP 30256); Campo Grande, *Hoehne & Gehrt s.n.* (SP 35760); Serra do Roncador, ca 210 km N of Xavantina, 500 m, *Irwin et al. 16087* (MICH, NY, UB), ca 87 km N of Xavantina, 550 m, *Irwin et al. 16484* (MICH, NY, UB), ca 60 km N of Xavantina, 550 m, *Irwin et al. 16681b* (MICH, NY); mun. Bataguaçu, 42 km de Porto de 15 de Novembro, *Krapovickas 14392* (C, CTES), *14396* (CTES); 23–40 km E de Aquiduana, *Krapovickas & Schinini 32918, 32893* (MICH); 4 km E de Ribas do Rio Pardo, *Krapovickas & Cristóbal 34372* (MICH); 6 km de Campo Grande, *Krapovickas & Cristóbal 34542* (MICH); Campo Grande, Lagôa Rica, 600–700 m, *Lutz s.n.* (R 72142); Chapada, *Moore 153* (BM); Campo Grande, *Occhioni 5775* (MICH); mun. Dourados, ca 20 km E of Itaum, *Pedersen 11116* (MICH); Fazenda Sta. Filomena, 56°40′W, 19°13′S, *Prance & Schaller 26269* (NY); 8 km NE of Base Camp (12°54′S, 51°52′W), ca 270 km N of Xavantina, *Ratter et al. 1990* (K); ca 200 km N of Xavantina, Xavantina-São Felix Road, *de Santos & Souza 1637* (K, MO, NY, P, RB, UB); Buriti, NE of Cuiabá, 2250 ft, *Smith 330* (K); mun. Campo Grande, Fazenda das Varzeas, *Sucre 10416* (RB); ca 10 km E of Campo Grande, *Swallen 9606* (US). Minas Gerais: 6 km N of Gouvêia on road to Diamantina, 1250 m, *Anderson 8564* (MICH, NY); mun. Belo Horizonte, Serra do Taquaril, *Barreto 7577* (F, US), *7578 p.p.* (F); Diamantina, *Brade 13776* (RB); Belo Horizonte, *Brade 14819 & Barreto 1335* (RB); Baú, *Brade 17802 & Altamira* (RB); Diamantina, *Brito 100* (R); *Claussen s.n.* (P-JUSS, lectotype of *P. lateritia*); *Claussen s.n.* (BR, G); Carandaí-Crespo, *Duarte 451* (RB); Patos de Minas, 800 m, *Duarte 2843* (RB); Cachambú, ca 1000 m, *Duarte 3787* (RB); rodovia Uberaba-Uberlândia, a 40 km de Uberaba, *Ferreira 2b* (UB 37618, holotype of *P. grandiflora*); rodovia Goiânia-Brasília, entre Uberaba e Uberlândia, *Ferreira 43* (NY, UB); *Gaudichaud 584* (P); Pouso Alegre, *Hoehne s.n.* (SP 19391); Serra do Espinhaço ca 25 km SW of Diamantina, on road to Gouvêia, 1300 m, *Irwin et al. 22091* (NY), ca 20 km SW of Diamantina, 1200 m, *Irwin et al. 22294* (MICH, NY); Ituiutaba, *Macêdo 38* (MO, S, SP), *2428* (BM, MO, S, US), *4962* (SP); Capão d'Antas, Nova Ponte, *Magalhães 241* (UB);

40 km 0 de Araguari, *Magalhães 19041* (NY); Diamantina, 1250 m, *Mexia 5798* (A, BM, G, GH, MO, NY, US); Belo Horizonte, *Porto & Fagundo 2200* (RB); Baependi, *Rabello 893* (R); Uberava [Uberaba], *Regnell II-28* (US), *II-28a* (S); Baguarí, *Regnell II-28d* (F, S, US); Caldas, *Regnell II-28e* (C, R, S); Passos, Serra de Ventania, *Regnell II-28x* (S); Serra do Curral, Belo Horizonte, *Roth 1591* (RB); *Schwacke s.n.* (R 72455); Serra da Mantiqueira, *Vidal 2054* (R); mun. Thermópolis, Chapadão do Jacuhy, *Vidal I-780, I-800, I-836* (R); José Alves, *Warming s.n.* (C); Lagôa Santa, *Warming s.n.* (C, F, LE, US); outskirts of Belo Horizonte, 1000 m, *Williams & Assis 5827* (GH); mun. Belo Horizonte, Morro das Pedras, 1100 m, *Williams & Assis 6938* (GH). Paraná: Fazenda Lagôa, ca 20 km N of Cianorte, *Anderson 11155* (MICH, NY, UB); mun. Campo Mourão, *Hatschbach 8819* (MICH, US); Fazenda Lagôa, Cianorte, *Hatschbach 14243* (F, MBM, MICH, NY, P, US), *21572* (MICH, P); Campo Mourão, *Labouriau 60* (SP). São Paulo: Mogi-Mirim, *Burchell 5090* (K), *5220* (GOET, K); Araras, *de Andrade s.n.* (SP 24514); Itirapina, *de Paula 111* (SP); Morro Pellado, *Edwall s.n.* (SP 12109); mun. Moji-Guaçu, Fazenda Campininha, ca 4 km NNW of Padua Sales, 575–650 m, *Eiten & Eiten 1901* (NY, SP, US), ca 10 km NNE of Padua Sales, *Eiten & Eiten 2280* (SP); mun. São Carlos, 3.5 km NNW of center of São Carlos, 21°59′S, 57°55′W, 825 m, *Eiten et al. 2914* (K, NY, SP, US); mun. Ibaté, 12.8 km NW of center of city of São Carlos, ca 1 km NE of Ibaté, *Eiten et al. 2928* (MO, NY, SP, US); mun. São Carlos, 13–15 km NW of Santa Eudóxia, *Eiten & Eiten 3291* (NY, SP, UB); mun. São Carlos, near boundary with mun. Araraquara, 19.9 km NW of railroad station at Santa Eudóxia, 625 m, *Eiten & Campos 3449* (NY, SP); mun. Moji-Guaçu, Fazenda Campininha, 6.2 km NNW of Padua Sales, 575–650 m, *Eiten & Eiten 5616* (NY), 10 km NNE of Padua Sales, *Eiten & Eiten 5701* (NY, UB, US); Itirapina, *Gehrt s.n.* (SP 8328); mun. Botucatu, 18 km N of Botucatu, 14 km E of São Miguel, ca 550 m, *Gottsberger 6571* (NY); caminho para Sete-Quedas, *Heiner 269* (S); Mogi-Mirim, *Hoehne s.n.* (SP 20525); Amparo, *Hoehne s.n.* (SP 20569); São Simão, *Kuhlmann 4144* (SP), *Lima 6268* (SP); Rio Claro, *Löfgren 587* (C); Sorocaba, *Lund s.n.* (C, UB); Itirapina, *Matos 92* (SP); mun. Moji-Guaçu, Fazenda Campininha, 10 km de Padua Sales, *Mattos 125 & Rizzini* (RB); mun. Moji-Guaçu, Fazenda Campininha, 3.2–3.4 km NNW de Padua Sales, *Mattos & Mattos 8305* (SP, US); São João de Boa Vista, *Mosén 4050* (P, S); Votuporanga, *Pires 57925* (NY, UB); inter Casa Branca et São Simão, *Regnell II-28b, II-28g* (S); Minas, *Riedel 584* (R); Sorocaba et Ypanama [Ipanema], *Riedel & Luschnath 2007* (A, GH, LE, NY, P, S, US); zwischen Rio Pirituba und Sorocaba, *Sellow IV. it. 5505* (NY, fragment, lectotype of *P. macrophylla*); prope Franca, *Wacket s.n.* (W). PARAGUAY: Cerro Cora, 36 km W of Pedro Juan Caballero, 300 m, *Anderson 11782* (MICH); 3 km N of Río Ypané on road to Pedro Juan Cabellero, 175 m, *Anderson 11790* (MICH); Est. Santa María, Cerro Noaga, *Anisits 2372* (S); dept. Kanendiju, col. Fortuna, 8 km de Kuruguatz, *Arenas 629* (CTES, MICH); dept. Paraguarí, Salto de Piraretá, *Arbo et al. 1750* (MICH); Cordillera de Altos, Cerro Chochá, *Fiebrig 390* (A, BM, F, G, K, M); Centurión, zwischen Río Apa und Río Aquidaban, *Fiebrig 4017* (BM, G, GH, K), *4590* (GH); San Luís, zwischen Río Apa und Río Aquidaban, 22–23°S, *Fiebrig 5181* (G, M); camino Bernal-Cué, *Hassler 1141* (G); Cordillera de Altos, *Hassler 2976* (BM, G, NY); Bernal-Cué, *Hassler 4055* (BM, G, K, NY, P); prope fl. Corrientes, *Hassler 4509* (BM, G, K, P); Ipé-hu, *Hassler 5054* (BM, G, K, NY, P); fl. Capibary, *Hassler 5927* (A, BM, F, G, K, MO, NY, P, S, W); prope Chololo, in valle fluminis Y-aca, *Hassler 6774* (A, BM, F, G, K, NY, P, S, W); Río Apa, *Hassler 8166* (A, BM, F, G, K, MO, NY, P, S, W), *8166a* (BM, F, G, K, NY); Sierra de Amambay, *Hassler 9881* (A, G, K, NY, P, W), *9881a* (GH, K), Conrados Estrella, *Hassler 10056* (G); dept. San Pedro, 43 km de San Estanislao Norte, *Krapovickas et al. 14265* (CTES, MO); dept. Paraguarí, Piraretá, *Schinini 4348* (F, MICH, P); dept. San Pedro, Ruta 3, 2 km S de Tacuara, *Schinini 8809* (MICH), 34 km N de Tacuara, *Schinini 8887* (MICH); dept. Amambay, camino entre Ruta 5 y Bella Vista, 9 km N de Ruta 5, *Schinini 8956* (MICH).

Peixotoa reticulata is a widespread taxon of which almost all of the known collections are apomictic. The anthers remain closed and contain mostly aborted pollen that is 80–97% non-staining in cotton blue in lactophenol. In a few exceptions this percentage is much lower (see also the section Apomixis). Rarely a few flowers of a specimen (e.g. *Fiebrig 4590*) will have a few or all of the anthers open. Pollen fertility may be higher than or the same as in samples from closed anthers. Only in two collections, *Mexia 5798* and *Occhioni 5775*, do all flowers have all anthers open. The pollen of *Mexia 5798* is 45–98% non-staining, while that of *Occhioni 5775* is almost 100% staining. The Occhioni collection is perhaps a rare, sexual individual.

Chromosome counts of the pollen mother cells of a collection from Paraguay (*Anderson 11790*) show that while 2n=30, the separation of anaphase I/telophase I is highly irregular. Most frequently 17 and 13 or 16 and 14 pairs would move to the opposite poles, but figures with 15 and 15 were also seen (W. R. Anderson, pers. comm.). In the only sexual species counted, *P. glabra* (*Anderson 11549*), n=10 (W. R. Anderson, pers. comm.). Since Gates (1981) found that

in *Banisteriopsis*, the most likely ancestor of *Peixotoa*, n=10 in nearly every count, this is probably also the base number for *Peixotoa*. *P. reticulata* may be the product of a cross between a diploid and a tetraploid. The resulting sterile triploid was then propagated apomictically. Such crosses may have happened several times. Also, as noted in the section on apomixis, it appears that hybridization between *P. reticulata* and sexual species does take place. Thus, *P. reticulata* as circumscribed here is probably polyphyletic. Such a history would account for its considerable morphological variation, which is reflected by a number of regional types. Their distinctions are summarized in Table I. These groupings are not abolutes, but indicate the combination of characters most likely to be encountered in each region. The extremes are quite distinct, yet are linked by many intermediate forms.

The samaras are extremely variable in the shape and the size of the wings. Those from the eastern part of the range tend to have the dorsal wing with the upper and lower margin straight or sigmoid and often parallel to each other. The lateral wings are 3–5 mm wide. Those from the more western part tend to have an arced or sigmoid upper margin and usually a semicircular or arced lower margin; their lateral wings are 4–7.5 mm wide. Perhaps these reflect hybridization with the large-winged *P. cordistipula* and *P. magnifica*. The variation in size is striking. In *Hatschbach 2465* from Terenos in southern Mato Grosso the dorsal wing is ca 3.5–4 cm long and ca 2–2.5 cm wide. The lateral wings are ca 1.6 cm high and ca 6–7 mm wide. In *Hatschbach 21770* from Rio Brilhante, south of Terenos, the dorsal wing is ca 1–1.5 cm long and ca 1 cm wide. The lateral wings are ca 6–6.5 mm high and ca 2 mm wide. These fruits appear immature or aborted, yet contain mature, apparently normal embryos.

In the past plants of *P. reticulata* from the western part of the range have often been assigned to *P. cordistipula* of central Mato Grosso and eastern Bolivia. This species differs from *P. reticulata* in its larger and persistent inflorescence stipules, longer staminode filaments, and the commonly present glandular mass in the center of the umbel. Also, the dense, white pubescence gives *P. cordistipula* a silvery-grey appearance.

Grisebach based his *P. reticulata* on two Sellow collections from east-central Minas Gerais. These were deposited at Berlin, but are no longer extant. A fragment of *Sellow III. it. c. 1310*, consisting of a leaf and flowers, is at NY and is here designated lectotype. Photographs of the Berlin specimen are at F, MICH, and NY. *Mexia 5798* is an excellent match for this collection. It is noteworthy that the flowers of the NY fragment have open anthers.

Collected in flower and fruit throughout the year.

26. Peixotoa sericea C. Anderson, sp. nov. Fig. 12.

Liana (?). Stipulae vegetativae deciduae, inflorescentiae 6–10 mm longae, acutae, persistentes. Petioli 8–10 mm longi. Laminae 7.1–10.3 cm longae, 3.3–5 cm latae, ellipticae vel anguste ellipticae, supra sparsim appresso-sericeae vel glabratae, subtus appresso-sericeae, biglandulosae 4.5–9 mm supra basim juxta vel prope costam. Folia inflorescentiae petiolo brevi, distaliora sessilia, linearia. Inflorescentia terminalis vel axillaris, umbellis singularibus. Bracteae bracteolaeque absentes. Pedicelli 13–15 mm longi. Sepala 3.8–4.5 mm longa. Limbus petalorum lateralium ca 10 mm longus, ellipticus, margine glanduloso-fimbriato. Limbus petali postici 6–6.5 mm longus, ellipticus vel anguste obovatus, margine glandulis capitatis ornato. Styli subaequales, 4–4.5 mm longi, anticus arcuatus versus petalum posticum, postici divergentes, inclinati versus petala postico-lateralia; stigmata capitata. Samara ignota.

Vine? Vegetative branches finely sericeous-tomentulose when very young, soon becoming glabrous. Stem stipules deciduous, not seen; inflorescence

Table I. Summary of the regional morphological types of *P. reticulata*.

	central Minas Gerais	western & southern Minas Gerais, & São Paulo	Paraná	Goiás	central Mato Grosso	southern Mato Grosso	Paraguay
shape of stem laminas	ovate, elliptical, suborbicular, rhombic	ovate, elliptical, suborbicular	ovate, elliptical, suborbicular	ovate, elliptical,	ovate, elliptical, lanceolate	ovate, elliptical	ovate, elliptical
abundance of hairs on lower surface of stem lamina	sparse to moderate	dense	moderate	moderate to dense	sparse to dense	sparse to dense	moderate
presence of petioles in inflorescence leaves	—	+/−	+ −	+ −	−	+	+
presence of secondary peduncle	rare	common	common	rare	rare	rare	almost always present
shape of limb of posterior petal	obovate, elliptical	obovate, orbicular	orbicular	obovate	elliptical	obovate	orbicular, oblate
margin of limb of posterior petal	capitate- or fimbriate-glandular	capitate-glandular	capitate-glandular	capitate- or fimbriate-glandular	capitate-glandular	capitate-glandular	capitate- or fimbriate-glandular
curvature of anterior style	arced toward posterior petal	arced toward posterior petal	arced toward posterior petal	arced toward posterior petal	slightly inclined toward posterior petal	erect or slightly inclined toward posterior petal	erect or slightly inclined toward posterior petal

stipules 6–10 mm long, 6–8 mm wide, cordate or triangular-cordate, apex acute, sparsely and finely velutinous or sericeous adaxially, sericeous abaxially, persistent. Stem leaves with the petiole 8–10 mm long, densely velutinous, laminas 7.1–10.3 cm long, 3.3–5 cm wide, elliptical or narrowly so, apex apiculate, base attenuate, sparsely appressed-sericeous to glabrous above, appressed-sericeous below, a pair of sessile glands borne 4.5–9 mm above the base at the costa or on the surface of the lamina up to 0.4 mm from the costa. Inflorescence leaves of the proximal nodes petiolate, the more distal sessile, laminas abruptly smaller than the cauline, the smallest not less than 2.2 mm long, 0.6 mm wide, the proximal narrowly elliptical, the distal linear, apex acuminate, glabrous above, densely sericeous-velutinous below, a pair of glands at the base at the costa or borne on the surface of the lamina up to 1 mm above the base, up to 0.4 mm from the costa, each gland 0.3–0.9 mm in diameter. Inflorescence terminal or axillary, the axes finely and densely tomentulose-velutinous, internodes of the primary axis 2–4 cm long, 2° axes 1.7–6.8 cm long, subsidiary axes absent; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts and bracteoles absent. Pedicels 13–15 mm long, densely golden velutinous. Sepals 3.8–4.5 mm long, 1.7–1.8 mm wide, velutinous adaxially, sparsely so near the base, glands 1.1–1.2 mm long, 0.7–0.8 mm wide. Claw of the lateral petals 2–2.2 mm long, limb ca 10 mm long, ca 7.5 mm wide, elliptical, base attenuate, fimbriae up to 0.4 mm long, glandular. Claw of the posterior petal ca 4 mm long, limb 6–6.5 mm long, 4.5–5 mm wide, elliptical or narrowly obovate, fimbriae up to 0.5 mm long, capitate-glandular. Filaments of the lateral stamens 4.5–4.8 mm long, posterior filament ca 3 mm long, strongly arced toward the posterior petal, anthers 1.3–1.4 mm long, glandular connectives 0.6–0.7 mm long. Pollen grains 42–50 μm. Anterior staminode filament 4.5–5 mm long, anterior-lateral filaments 3.3–4 mm long, posterior-lateral filaments 3–3.3 mm long, always shorter than the anterior lateral two, inflexed between the posterior styles, anterior and anterior-lateral glands ca 1.2–1.3 mm long, ca 1.1–1.2 mm wide, posterior-lateral glands ca 1 mm long, ca 0.8 mm wide, all glands with the apex and abaxial face smooth. Styles 4–4.5 mm long, ca 0.3 mm wide, anterior style arced toward the posterior petal, posterior styles divergent, inclined toward the posterior-lateral petals, all styles densely pubescent with basifixed hairs in the proximal ⅓ of their lengths, stigmas ca 0.3–0.4 mm in diameter, capitate. Samara not seen.

Type. *Eupunino 120.* Brazil. Bahia: Santa Cruz de Cabrália, Reserva Biológica do Pau-brasil, 5 Jan 1972 (holotype CEPEC, isotype MICH).

Peixotoa sericea is known only from the type (Fig. 10). It is one of two species in the genus with sericeous leaves. The hairs are sessile or subsessile and have a straight, stiff trabecula. The lamina is very sparsely pubescent above but more densely so below. Yet, to the naked eye the leaves may appear glabrous. The leaves are also atypical for the genus in that the base is cuneate instead of cordate or subtruncate. The glands of the stem leaves are borne above the base but at the costa, usually at different levels from each other. *P. adenopoda,* the other species with sericeous leaves, differs in that the leaf glands are stalked and borne on the surface of the lamina away from the base and costa. Also, the terminal inflorescence nodes bear three umbels, i.e., are 12-flowered. Those of *P. sericea* bear a single umbel and thus are 4-flowered.

Unfortunately, the collector of the type did not note the habitat. According to Mori and Silva (1979), the reserve at Santa Catarina Cabrália consists largely of *mata higrófila* (tropical wet forest). Perhaps *P. sericea* grows at the forest edge or in the adjacent restingas. Cerrado, the vegetation type in which *Peixotoa* is most commonly collected, is not found in this area.

Peixotoa hispidula is the only other coastal species in Bahia. It has the typically

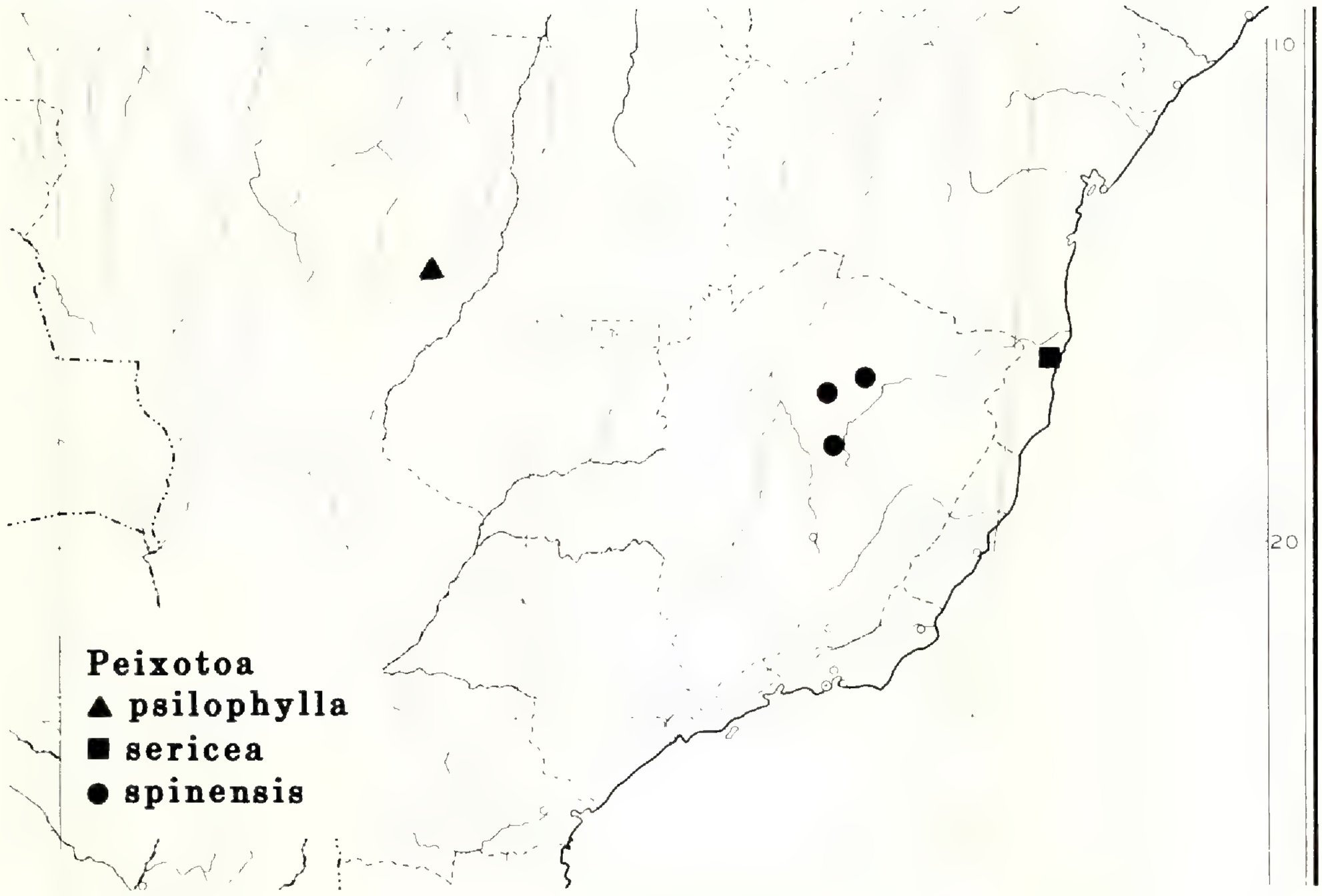

FIG. 10. Distribution of *P. psilophylla*, *P. sericea*, and *P. spinensis*.

cordate leaves which are usually glabrous or nearly so or may be variously pubescent but never sericeous. Its large flowers are borne in a solitary umbel or in only slightly more elaborate inflorescences.

27. Peixotoa spinensis C. Anderson, sp. nov. Fig. 16.

Frutex vel suffrutex caulibus usque ad 2 m longis, prostratis, ascendentibus vel volubilibus. Stipulae vegetativae 3–10.5 mm longae, cordatae vel triangulares, acutae vel bifidae, deciduae interdum persistentes. Petioli 2–8 mm longi. Laminae 3.6–9.3 cm longae, 1.8–6.5 cm latae, ellipticae vel ovatae vel lanceolatae, supra velutinae raro tomentoso-velutinae, subtus tomentosae vel lanatae, ferentes 2 (interdum 3–4) glandulas (2.2–)3–20 mm supra basim 0–14 mm a costa. Folia inflorescentiae petiolo brevi raro sessilia, linearia vel subulata. Inflorescentia terminalis vel axillaris, umbellis singularibus. Bracteae bracteolaeque praesentes. Pedicelli 8–28 mm longi. Sepala 3–6.1 mm longa. Limbus petalorum lateralium 9.5–13.5 mm longus, orbicularis, margine glanduloso-fimbriato vel glanduloso-denticulato, interdum praesertim apice eglanduloso. Limbus petali postici 6–8.3 mm longus, ellipticus vel late ellipticus, raro suborbicularis, margine glandulis capitatis ornato vel apice glanduloso-fimbriato. Glandulae staminodiorum apice profunde indentatae, indentatione in pagina abaxiali decurrenti, interdum postico-lateralibus laevibus. Stylus anticus 3.1–4.2 mm longus, erectus vel parum inclinatus versus petalum posticum, styli postici 3.4–4.5 mm longi, semper anticum excedentes, divergentes, inclinati versus petala postico-lateralia; stigmata capitata. Ala dorsalis samarae ca 2 cm longa, ca 1.4 cm lata, alae laterales 2.3–3.5 mm latae, 7.3–8 mm altae.

Shrub or subshrub with ascending, twining or prostrate stems to 2 m. Vegetative branches densely tomentulose-velutinous, pubescence abraded from older parts. Stem stipules 3–10.5 mm long, 3.5–10 mm wide, cordate or triangular, entire with the apex acute, or bifid, finely velutinous-tomentulose,

sparsely so adaxially, densely so abaxially, deciduous or sometimes persistent; inflorescence stipules like the cauline, sometimes more densely pubescent, deciduous. Stem leaves with the petioles 2–8 mm long, densely tomentose-velutinous, laminas 3.6–9.3 cm long, 1.8–6.5 cm wide, elliptical or ovate to lanceolate, apex apiculate or in narrow leaves acuminate, base cordate, velutinous or rarely velutinous-tomentose above, tomentose or woolly below, a pair of sessile glands borne on the surface of the lamina (2.2–) 3–20 mm above the base, up to 14 mm from the costa, sometimes with one or two additional glands, each gland 0.5–1.5 (–2.3) mm in diameter. Inflorescence leaves with the petiole 0.2 mm or more long, rarely sessile, laminas abruptly smaller than the cauline, the smallest not less than 1.4 mm long, 0.7 mm wide, shape of the more proximal like the cauline, the more distal lanceolate to linear to subulate, apex acuminate, velutinous or sparsely so adaxially, densely velutinous abaxially, a pair of glands borne on the surface of the lamina in the larger leaves, at the base at the costa or halfway on the petiole in the smaller leaves, each gland 0.3–1.3 mm in diameter, sometimes with one or two smaller glands (0.4–0.6 mm in diameter) above, below or adjacent to the larger pair. Inflorescence terminal or axillary, the axes tomentulose-velutinous, internodes of the primary axis 2–8.5 cm long, 2° axes 1.9–8.7 cm long, 2° subsidiary axes 1.2–2 cm long, 3° axes 0.7–3.3 cm long; umbels 4-flowered, one umbel per node, primary and secondary peduncles absent. Bracts 0.3–1.6 mm long, 0.2–0.7 mm wide, linear, triangular or sometimes semicircular, glabrous, sometimes velutinous on the margins; bracteoles 0.1–0.5 (–0.7) mm long, 0.1–0.4 mm wide, triangular or semicircular, glabrous. Pedicels 8–28 mm long, densely tomentulose-velutinous, the smaller ones up to twice again as long in fruit. Sepals 3–6.1 mm long, 1.6–3.5 mm wide, adaxially the proximal ½–⅔ glabrous, the distal ½–⅔ tomentulose, glands 1–2.1 mm long, 0.7–1.2 mm wide. Claw of the lateral petals 2.5–3.5 mm long, limb 9.5–13.5 mm long, 10–13 mm wide, orbicular, base attenuate, fimbriate and/or denticulate, fimbriae and teeth up to 0.4 mm long, glandular, sometimes eglandular, especially at the apex. Claw of the posterior petal 3.2–4.3 mm long, limb 6–8.3 mm long, 5.2–7.2 mm wide, elliptical or broadly so, rarely suborbicular, fimbriae up to 0.3 (–0.5) mm long, capitate-glandular, sometimes the apex fimbriate-glandular. Filaments of the lateral stamens 3.5–4.6 mm long, posterior filament 3.2–4 mm long, always shorter than the lateral four, arced toward the posterior petal, anthers 1.1–1.4 mm long, glandular connectives 0.6–0.8 mm long. Pollen grains ca 50 μm. Filament of the anterior staminode 3.5–4 mm long, always exceeding the anterior-lateral two, anterior-lateral filaments 3.2–3.8 mm long, always exceeding the posterior-lateral two, posterior-lateral filaments 3–3.5 mm long, inflexed between the posterior styles, anterior and anterior-lateral glands 1.2–1.4 mm long, 1.2–1.5 mm wide, the anterior gland often a little larger than the anterior-lateral two, posterior-lateral glands 0.8–1.2 mm long, ca 1 mm wide, all glands with an indentation across the apex and abaxial face or sometimes the posterior-lateral two smooth. Anterior style 3.1–4.2 mm long, 0.3–0.4 mm wide, always shorter and a little stouter than the posterior two, erect or very slightly inclined toward the posterior petal, posterior styles 3.4–4.5 mm long, ca 0.3 mm wide, divergent, inclined toward the posterior-lateral petals, all styles glabrous or sometimes with scattered hairs in the proximal ⅓ of their lengths, stigmas 0.4–0.5 mm in diameter, capitate. Carpophore up to 1.7 mm long. Torus up to ca 4.5 mm high. Samara with the dorsal wing ca 2 cm long, ca 1.4 cm wide, upper margin arced, lower margin straight, slightly erose, lateral wings 2.3–3.5 mm wide, 7.3–8 mm high, rectangular, margin erose to lacerate, areole 4.2–4.5 mm long and wide, nut ca 5.6 mm long, ca 3.5 mm in diameter, mature seeds not seen.

Type. *Anderson 8730*. Brazil. Minas Gerais: Serra do Espinhaço, 25 km by

road NE of Diamantina, ca 1.5 km from Rio Jequití, 790–900 m, 12 Apr 1973 (holotype UB, isotypes MICH, NY).

Distribution. (Fig. 10). Known only form the northern and central part of the Serra do Espinhaço of Minas Gerais; cerrado.

BRAZIL. Minas Gerais: 25 km by road E of Diamantina, 2 km W of Rio Jequití, 790 m, *Anderson 8364* (MICH, NY, UB); estrada para Grão Mogul, *Graziela [Barroso] s.n.* (RB 171697); mun. Grão Mogul, Rio Itacambiruçu, *Hatschbach 41240* (MICH); mun. Grão Mogul, rod. Cristalia, *Hatschbach 41394* (MICH); ca 18 km W of Grão Mogul, 950 m, *Irwin et al. 23662* (MICH, NY, UB); ca 3 km N of São João da Chapada, 1200 m, *Irwin et al. 28236c* (NY); slopes N of Grão Mogul, *Maguire 49285* (MICH, NY); entre Montes Claro e Riacho dos Machados, *Santos s.n.* (NY).

Peixotoa spinensis is easily recognized by the leaf glands that are borne on the surface of the lamina away from the base and costa. The laminas are densely tomentose or woolly below. All or only the anterior and anterior-lateral staminode glands have an indentation across the apex and decurrent on the abaxial face. *P. paludosa* is the only other species of the Serra do Espinhaço in which the leaf glands are borne on the surface of the lamina. It differs in that its leaves are only moderately pubescent and in that its staminode glands are smooth. Also, its inflorescence stipules are usually persistent at the more distal nodes. The inflorescence stipules and also commonly the inflorescence leaves of *P. spinensis* are deciduous. The larger leaves of *P. leptoclada* sometimes have the glands borne on the lamina but usually in addition to a basal pair. *P. leptoclada* is distinguished by its large (at least 7 mm long), persistent inflorescence stipules.

Collected in flower in February through April, also in August and September, in fruit in February.

28. Peixotoa tomentosa Adr. Jussieu in St. Hilaire, Fl. Bras. Mer. **3**: 61. 1832 [1833]. Fig. 18.

P. tomentosa β *oligothrica* Adr. Jussieu in St. Hilaire, Fl. Bras. Mer. 3: 62. 1832 [1833]. Type. *St. Hilaire 392* (lectotype P!).

P. tomentosa β *rotundifolia* Grisebach, Linnaea 13: 212. 1839. Type. *Sellow s.n.* [*Sellow III. it. B1840 c1306* (26 Dec 1818), fide Niedenzu, 1912] (holotype B, destroyed, fragment of holotype, NY!).

P. phlomoides Adr. Jussieu, Ann. Sci. Nat. Sér. II, Bot. 13: 280. 1840. Type. *Martius s.n.* (holotype M!).

P. tomentosa f. 2. *cuneata* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 38. 1912. Type. *Sellow* IV. it. *5504* (lectotype NY!).

P. tomentosa f. 3. *gracilior* Niedenzu, Verz. Vorles. Akad. Braunsberg W-S 1912–1913: 38. 1912. Type. *Glaziou 16731* (lectotype C!, isotypes BR! K! LE! P! R!).

Erect, ascending or prostrate shrub or subshrub to 2 m. Vegetative branches loosely or densely golden velutinous or velutinous-tomentose when young, pubescence faded to white and often abraded from older parts. Stem stipules (2.5–) 3.1–9.5 mm, 3.2–10 mm wide, cordate or cordate-triangular or triangular, entire with the apex acute or notched, or bifid, glabrous or finely velutinous or tomentulose adaxially, densely velutinous-tomentulose abaxially, deciduous; inflorescence stipules like the cauline, sometimes a little larger, usually more densely pubescent, often persistent. Stem leaves with the petiole (1–) 2–9 mm long, densely golden velutinous or velutinous-tomentose, lamina 4.5–10.8 cm long, 2.6–8.7 cm wide, ovate or elliptical or suborbicular or sometimes narrowly elliptical or lanceolate or oblanceolate or rhombic, apex apiculate, base cordate or slightly cordate or almost truncate, densely golden velutinous above, tomentose or sometimes also pubescent with T-shaped hairs or woolly below, a pair of

sessile glands at the base at the costa or halfway on the petiole or sometimes on the petiole just below the lamina, each gland 0.8–2 (–2.5) mm in diameter. Inflorescence leaves with the petiole 0.5 mm or more long or the most distal subsessile or sometimes sessile, laminas abruptly smaller than the cauline, the smallest not less than 3.8 mm long, 1 mm wide, shape of the more proximal like the cauline, the more distal lanceolate or linear, the most distal sometimes subulate, apex acuminate or caudate, velutinous or sparsely so above, densely velutinous or velutinous-tomentulose below, a pair of glands at the base at the costa or halfway on the petiole or rarely on the petiole just below the lamina, each gland 0.8–1.8 mm in diameter, sometimes with a second, usually smaller, pair (0.3–1.3 mm in diameter) immediately above the pair of larger glands. Inflorescence terminal, the axes densely golden velutinous or velutinous-tomentulose, internodes of the primary axes 1.5–8.8 cm long, 2° axes 1.4–18.3 cm long, 3° axes 2.4–3.5 cm long, subsidiary axes absent, usually at the more distal nodes the 2° and 3° axes suppressed, with 1 or 2 umbels sessile or borne on secondary peduncles in the leaf axil, always with 3 umbels at the terminal nodes, each umbel 4-flowered, primary peduncles absent, secondary peduncles up to 12.5 cm long or absent. Bracts 0.6–1.8 mm long, 0.3–0.8 mm wide, triangular or narrowly triangular, usually glabrous, sometimes tomentulose abaxially or on the margins; bracteoles 0.1–1 mm long, 0.1–0.3 mm wide, triangular or narrowly triangular or semi-circular, usually glabrous, sometimes sparsely tomentulose on the margins; bracts and/or bracteoles sometimes absent. Pedicels 8–21 (–29) mm long, densely golden velutinous or velutinous-tomentulose, sometimes a little longer in fruit. Sepals 3.3–6 mm long, 1.9–2.8 mm wide, adaxially velutinous or tomentulose or pubescent only in the distal 1/8–1/2, the proximal 1/2–7/8 glabrous, glands 1.2–2.2 mm long, 0.8–1.3 mm wide. Claw of the lateral petals 1.5–2.7 mm long, limb 9.5–12.3 mm long, 10–11 mm wide, orbicular or broadly elliptical, base briefly attenuate, fimbriae up to 0.5 mm long, glandular or eglandular. Claw of the posterior petal 3–3.5 mm long, limb 6.6–9.5 (–10.2) mm long, 5.9–9 (–9.6) mm wide, orbicular or broadly obovate, fimbriae up to 0.7 (–1) mm long, capitate-glandular in the proximal ½–⅔, the distal ⅓–½ fimbriate-glandular. Lateral stamen filaments 3.2–4.5 mm long, usually subequal, sometimes the posterior-lateral filaments longer or shorter than the anterior-lateral two, posterior filament 2.8–4 mm long, usually shorter than the lateral four, arced toward the posterior petal, anthers 1–1.2 (–1.4) mm long, glandular connectives 0.6–0.9 mm long. Pollen grains ca 50 μm. Anterior staminode filament 3.7–4.7 mm long, exceeding the anterior-lateral two at least slightly, anterior-lateral filaments 3.2–4.3 mm long, usually longer than or sometimes subequal to the posterior-lateral two, posterior-lateral filaments 3.1–4 mm long, inflexed between the posterior styles, anterior and anterior-lateral glands 1.1–1.4 mm long, 1.1–1.4 m wide, the anterior gland often a little larger than the anterior-lateral two, posterior glands 1.1–1.2 mm long, 0.8–1.2 mm wide, always a little smaller than the anterior three, all glands with the apex and abaxial face smooth. Anterior style 3.4–4.2 mm long, 0.3–0.4 mm wide, equal to or exceeding the posterior two, arced toward the posterior petal, posterior styles 3.2–4 mm long, 0.2–0.3 mm wide, divergent, inclined toward the posterior-lateral petals, stigmas 0.3–0.5 mm in diameter, capitate. Carpophore up to 2.8 mm long. Torus up to ca 5 mm high. Samara with the dorsal wing 1.5–2.2 cm long, 1.1–1.5 cm wide, upper margin straight, sigmoid or arced, lower margin arced, erose, lateral wings 2.3–5.2 mm wide, 7.2–14 mm high, rectangular or semicircular, slightly erose, areole 2.2–5 mm long, 2.5–4 mm wide, nut 3.5–6 mm long, 2.8–4.5 mm in diameter, seed 5.8–7 mm long, outer cotyledon 4.9–7.9 mm long, 1.8–2.3 mm wide, folded at ⅔–¾ of its length, inner cotyledon 4.5–6.1 mm long, 1.6–2.2 mm wide, folded at 2/3–4/5 of its length.

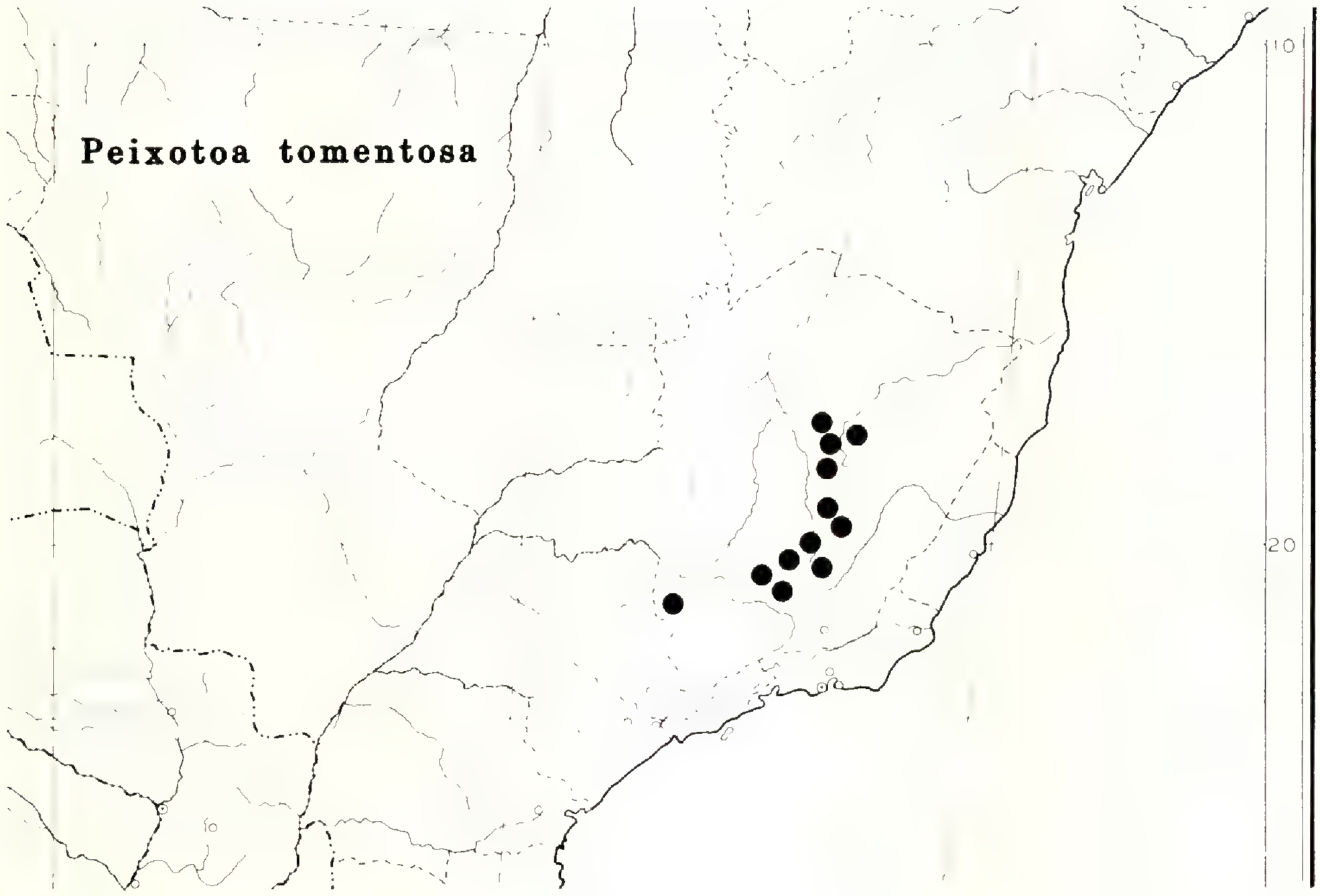

FIG. 11. Distribution of *P. tomentosa*.

Type. *St. Hilaire s.n.* Brazil. Minas Gerais: "In montibus . . . Serra da Caraça et Serra d'Ouro Branco necnon pagum Nossa Sñra da Penha (Minas Novas) . . ." (lectotype P!).

Distribution. (Fig. 11). Known mostly from the central section of the Serra do Espinhaço of Minas Gerais; cerrado, campo, and along gallery forests.

BRAZIL. Minas Gerais: 12 km by road W of Diamantina on road to Curvelo, 1450 m, *Anderson 8430* (MICH, NY); 7 km W of Diamantina, KM 299 on MG-259, 1350 m, *Anderson 35155* (MICH, NY); mun. Belo Horizonte, Serra do Taquaril, *Barreto 7578 p.p.* (RB), *7622* (F); São Sebastião do Paraíso, Morro do Liso, *Beta 97* (R); Belo Horizonte, *Brade 11822* (R); São Sebastião do Paraíso, Baú, *Brade 17810 & Altamira* (RB); Ouro Preto, *Campos s.n.* (SP 18825); circa Cachoeira do Campo, *Casaretto 2711* (G); Ouro Branco, *Castellanos 25616 et al.* (NY); *Claussen 14* (P), *35* (G, P), *75A* (BR), *76A* (BR), *131* (BM, BR, GH, MO, S, W), *131c* (W), *141* (BM), *157* (BM), *197* (BR, G, P, W), *414* (BR, G, W); de Rodrigo Silvio, *Damazio 922* (G); ca 50 km N of Congonhas along highway 135 to Belo Horizonte, 1270 m, *Davidse & Ramamoorthy 10795* (MICH, MO); mun. Ouro Preto, between Itabirita and Belo Horizonte, KM 15, ca 1200 m, *Davis & Shepherd D59601* (E); Serra do Cipó, KM 132, 1330 m, *Duarte 2206* (RB, S); Serra do Cipó, mun. Jaboticatubas, along road at KM 111, 19°19'S, 43°36'W, 1000–1050 m, *Eiten & Eiten 6837* (K, NY, UB, US), along road at KM 116–117 from Almeida to Conceição do Mato Dentro, 1150 m, *11072* (MICH); mun. Caeté, fazenda Geriza, *Felippe 31* (SP, US); Serra da Pinheiro, près de São João del Rei, *Glaziou 16731* (BR, C, K, LE, R); Serra d'Ouro Branco, São Julião, *Glaziou s.n.* (BM, P); Serra do Cipó, mun. Santa Ana do Riacho, *Hatschbach 35286* (MICH); Serra São João del Rei, Itacolumit, *Helmenreichen s.n.* (W); Miguel Burnier, *Hoehne s.n.* (SP 5117); Serra do Itabarito, ca 45 km SE of Belo Horizonte, ca 1500 m, *Irwin et al. 19514* (MICH, NY); Serra do Cipó, ca KM 112, ca 135 km N of Belo Horizonte, 1200 m, *Irwin et al. 20436* (MICH, NY); ca 18 km NE of Diamantina on road to Mendanha, 1300 m, *Irwin et al. 22676* (MICH, NY); ca 7 km NE of Diamantina on road to Mendanha, 1300 m, *Irwin et al. 22833* (MICH, NY); 8 km E of Diamantina, 1175 m, *Irwin et al. 27661* (MICH, NY); ca 3 km N of São João da Chapada, 1200 m, *Irwin et al. 28236a* (MICH, NY); Serra da Caraça, 10 km W of Barão de Cocais, 1400 m, *Irwin et al. 28891* (MICH, NY), *28976* (NY), *29081* (MICH, NY); Serra do Cipó, mun. Jaboticatubas, KM 123 rodovia Lagôa Santa-Conceição do Mato Dentro-Diamantina, *Joly & Semir 3592* (E.), KM 112 rodovia Lagôa Santa-Conceição do Mato Dentro-Diamantina, *Joly et al. 1009, 1401* (E); mun. Ouro Preto, 1150 m, *Krapovickas & Cristóbal 33538* (MICH); Serra do Cipó, *Kuhlmann & Edmundo 8* (RB); Belo Horizonte, *Labouriau 1013* (RB); *Langsdorff s.n.* (LE, P); Serra da Caraça, Santa Bárbara, *Leithao Filho et al. 9568* (BM); Serra do São José, São João del Rei, *Lutz 45* (R); Serra do

Itatiaia, Ouro Preto, *Magalhães 1124* (RB); Serra Rola Moça, Betim, *Magalhães 17015* (MICH); Serra do Curral e Mutuca, Nova Lima, *Magalhães 19496* (UB); Serra Rola Moça, 8 km from Belo Horizonte, 4300 ft, *Maguire 44619* (MICH, NY); 3 mi from Diamantina on road to Curvelo, 4300 ft, *Maguire 44770* (MICH, NY); Serra do Mutuca, Belo Horizonte, 1200 m, *Markgraf et al. 3541* (F, RB); Serra do Taquaril, Belo Horizonte, *Markgraf et al. 3585* (RB); Congonhas do Campo, *Martius s.n.* (M, holotype of *P. phlomoides*); Serro Frio, Sepes, *Martius s.n.* (M); Cachoeira do Campo, *Martius 1168* (BR, G, LE, M, NY); prope Sabará, *Netto 80* (R); Serra da Moeda, 26 km de Belo Horizonte, 1300 m, *Pabst 7117* (NY); Pico de Itabirito, 1400–1600 m, *Palacios et al. 3853* (R); Serra do Curral, *Pereira 2462 & Pabst 3298* (RB); Serra da Moeda, BR-3, *Pereira 7525* (M); ad Oliveira, *Pohl 358* (F, NY, W); Ouro Branco, *Porto 1259* (RB); Tejuco [Diamantina], *Riedel 1258* (LE, S, US); *Riedel XIII* (LE, S); Cachoeira do Campo, *Riedel s.n.* (BR); Penha, *St. Hilaire s.n.* (P, syntype of *P. tomentosa*); Serra da Carassa [Caraça], *St. Hilaire s.n.* (P, syntype of *P. tomentosa*); Serra d'Ouro Branco, *St. Hilaire s.n.* (P, syntype of *P. tomentosa*); *St. Hilaire s.n.* [392] (P, lectotype of *P. tomentosa β oligothrica*); São Julião, *Schwacke s.n.* (R 19579); Pico d'Itabira, *Schwacke s.n.* (R 72391); Serra do Cipó, mun. Jaboticatubas, KM 110, rodovia Lagôa Santa-Conceição do Mato Dentro-Diamantina, *Sazima & Semir 3843* (E); Serra da Moeda, *Sellow B1840 c1306* (NY, fragment of holotype of *P. tomentosa β rotundifolia*); Serra do Cipó, mun. Jaboticatubas, KM 112, rodovia Lagôa Santa-Conceição do Mato Dentro-Diamantina, *Semir & Sazima 564* (E); Serra do Pinheiro, *Silveira 21* (R, RB); Serra do São João del Rei, 3500–5500 ft, *Stephan s.n.* (K); Belo Horizonte, *Texeira s.n.* (SP 18829); Serra do Curral, mun. Belo Horizonte, *Vidal s.n.* (R 129614, R 129617); Serra do Cipó, Chapéu de Sol, 1060 m, *Vidal II-6302, V-6* (R); Serra do Cipó, Fazenda do Cipó, *Vidal V-75, V-91* (R); *Weddell 1208 p.p.* (G, P); vicinity of Lagôa Seca, 20 km S of Belo Horizonte, *Williams 5458* (GH); mun. Betim, Serra da Caveira, 1600 m, *Williams & Assis 6238* (BR, GH); Serra do Mutuca, mun. Belo Horizonte, ca 8 km beyond Lagôa Seca, 1100 m, *Williams & Assis 6281* (GH); Serra do Curral, mun. Nova Lima, 1300 m, *Williams & Assis 6394* (GH); mun. Nova Lima, Lagôa Grande, 1300–1500 m, *Williams & Assis 6536* (GH, SP, US); mun. Nova Lima, Pico de Belo Horizonte, 1300 m, *Williams & Assis 7147* (GH); mun. Betim, Serra da Caveira, 1300 m, *Williams & Assis 7494* (F, GH, MO, NY, S).

Peixotoa tomentosa is readily recognized by its inflorescence structure. Each terminal node bears three, commonly sessile, umbels and thus is 12-flowered. At the more distal nodes the secondary and tertiary axes are usually suppressed and one or two umbels are borne sessile or on secondary peduncles in each leaf axil. The young branches, the petioles, and the inflorescence axes are densely golden velutinous or velutinous-tomentulose. The leaves are golden velutinous above and usually densely white or greyish tomentose or woolly below. The hairs of the lower surface are often so abundant that the epidermis is obscured and only the larger veins and costa are visible. The leaves vary in shape from ovate to broadly or narrowly elliptical to obovate to suborbicular to rhombic or less commonly to lanceolate or oblanceolate. Plants from the Serra do Cipó, especially, tend to be more robust than others and are more likely to have suborbicular or broadly ovate laminas. However, this variation extends throughout the range and does not justify recognition of infraspecific taxa. Niedenzu also recognized a form, *gracilior*, for plants with particularly long and slender pedicels, which are indeed striking. However, the size of the pedicel is highly variable in this and all other species.

Three other species have a similar inflorescence structure, but none are as densely pubescent as *P. tomentosa*. *P. adenopoda* of east-central Bahia differs in that its leaf glands are stalked and borne on the surface of the lamina away from the base and costa, and in that its staminode glands have an indentation across the apex and decurrent on the abaxial face. In *P. catarinensis*, from coastal Santa Catarina, the leaf glands are also borne on the lamina but are very small, 0.2–0.7 mm in diameter. In *P. tomentosa* the staminode glands are smooth. The leaf glands are sessile, 0.8–2.5 mm in diameter, and borne at the base at the costa or halfway on the petiole or sometimes on the petiole just below the lamina. The northern range of *P. parviflora* coincides with the range of *P. tomentosa*. *P. parviflora* is probably a close relative and the species most likely to be confused with *P. tomentosa*. Its flowers, which are smaller than those of *P. tomentosa*, are unusual in that the posterior styles curve toward the anterior-lateral petals instead of toward the posterior-lateral petals. The pubescence of the inflorescence

branches is commonly white, though sometimes golden, and much sparser. The inflorescence leaves are always petiolate, never sessile as is common in *P. tomentosa,* and the umbels are always borne on secondary peduncles.

Collected in flower throughout the year, in fruit from November through April and in July.

EXCLUDED AND DOUBTFUL SPECIES

P. cordobensis Kuntze, Rev. Gen. 3(2): 28. 1898. *Cordobia argentea* (Grisebach) Niedenzu, Verz. Vorles. Ak. Braunsberg 1912–1913: 41. 1912.

See section *Relationships within the Family.*

P. microphylla Turczaninow, Bull. Soc. Nat. Moscow 36(1): 584. 1863.

According to Turczaninow, the type of this species was collected by "Hoker" or "Loker" and was seen by him in Robert Brown's herbarium. All attempts to locate this type have been unsuccessful. The description is too vague to allow this name to be assigned to any known species of *Peixotoa.* Perhaps the type does not belong to this genus at all. The author does not mention such structures as the cordate stipules, the four-flowered umbels or the unique androecium. Moreover, in his brief discussion, he does speak of pedicels that are bibracteolate in the middle, a condition unknown in *Peixotoa.*

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ACKNOWLEDGMENTS

I am grateful to W. R. Anderson for his generous advice, his numerous valuable suggestions and comments, and for providing the chromosome counts. I also wish to thank Stuart R. Lowrie, who shared his insights concerning the nature of malpighiaceous pollen, and who supplied the SEM micrographs. Bronwen Gates kindly permitted me to consult her [then] unpublished monograph of *Banisteriopsis*. The handsome illustrations were drawn by Karin Douthit.

I am also indebted to the curators of the following herbaria who provided access to their collections and arranged for loans: A and GH (Harvard), BM (London), BR (Brussels), C (Copenhagen), CEPEC (Itabuna), CTES (Corrientes), E (Edinburgh), F (Chicago), G (Geneva), GOET (Göttingen), IAN (Belém), K (Kew), LAM (Los Angeles), LE (Leningrad), M (Munich), MBM (Curitiba), MG (Belém), MO (St. Louis), NY (New York), P (Paris), R, RB, and RFA (Rio de Janeiro), S (Stockholm), SP (São Paulo), U (Utrecht), UB (Brasília), US (Washington), and W (Vienna).

This work was supported by grant G-DEB-79-04946 from the National Science Foundation to the University of Michigan.

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P. lateritia Adr. Juss. 62
P. leptoclada Adr. Juss. 5, 10, 14, 16, **47–49**, 51, 56, 71, 85
P. macrophylla Griseb. 62
P. macrophylla f. I. *minor* (Nied.) Nied. 62
P. macrophylla f. II. *typica* (Griseb.) Nied. 62
P. magnifica C. Anderson 8, 9, 10, 12, 16, 32, 47, **49–52**, 53, 66, 88
P. megalantha C. Anderson 15, 51, **52–53**, 90
P. microphylla Turcz. 75
P. octoflora C. Anderson 6, 10, 11, 13, **54–55**, 59, 90
P. paludosa Turcz. 5, 9, 10, 14, 16, 25, 49, 51, **55–57**, 71, 84
P. parviflora Adr. Juss. 6, 8, 9, 12, 14, 18, 21, 26, 28, **57–60**, 74, 87
P. parviflora var. β *primaeva* Nied. 55, 57
P. phlomoides Adr. Juss. 71
P. psilophylla C. Anderson 3, 13, 40, **60–62**, 69, 90
P. reticulata Griseb. 6, 9, 10, 12, 13, 14, 32, 35, 38, 53, **62–67**, 91, 92
P. sericea C. Anderson 3, 5, 9, 11, 14, 25, 29, **66**, **68–69**, 81
P. spinensis C. Anderson 5, 16, 26, 29, 56, **69–71**, 85
P. tomentosa Adr. Juss. 6, 14, 18, 21, 26, 28, 29, 60, **71–75**, 87
P. tomentosa f. 2. *cuneata* Nied. 71
P. tomentosa f. 3. *gracilior* Nied. 71
P. tomentosa β *oligothrica* Adr. Juss. 71
P. tomentosa β *rotundifolia* Griseb. 71
Stigmaphyllon Adr. Juss. 3

FIG. 12. *P. adenopoda*, *P. sericea* and *P. jussieuana*. a–e, *P. adenopoda*: a) flowering branch and stem leaf, × 0.5, detail x 2.5; b) leaf gland, x 5; c) base of a distal umbel, × 2.5; d) flower, × 2.5; e) posterior-lateral (left) and anterior (right) staminodes, × 5. f–h, *P. sericea*: f) flowering branch and stem leaf, × 0.5, detail × 2.5; g) base of a distal umbel, × 2.5; h) flower, x 2.5. i–l, *P. jussieuana*: i) flowering branch and stem leaf, × 0.5, detail × 2.5; j) flower, × 2.5; k) anterior (left) and posterior-lateral (right) staminode glands, × 10; l) samara, × 1. a–e from *Jesus 392*, f–h from *Eupunino 120*, i–k from *Eiten & Eiten 4835*, l from *Lützelburg 275*.

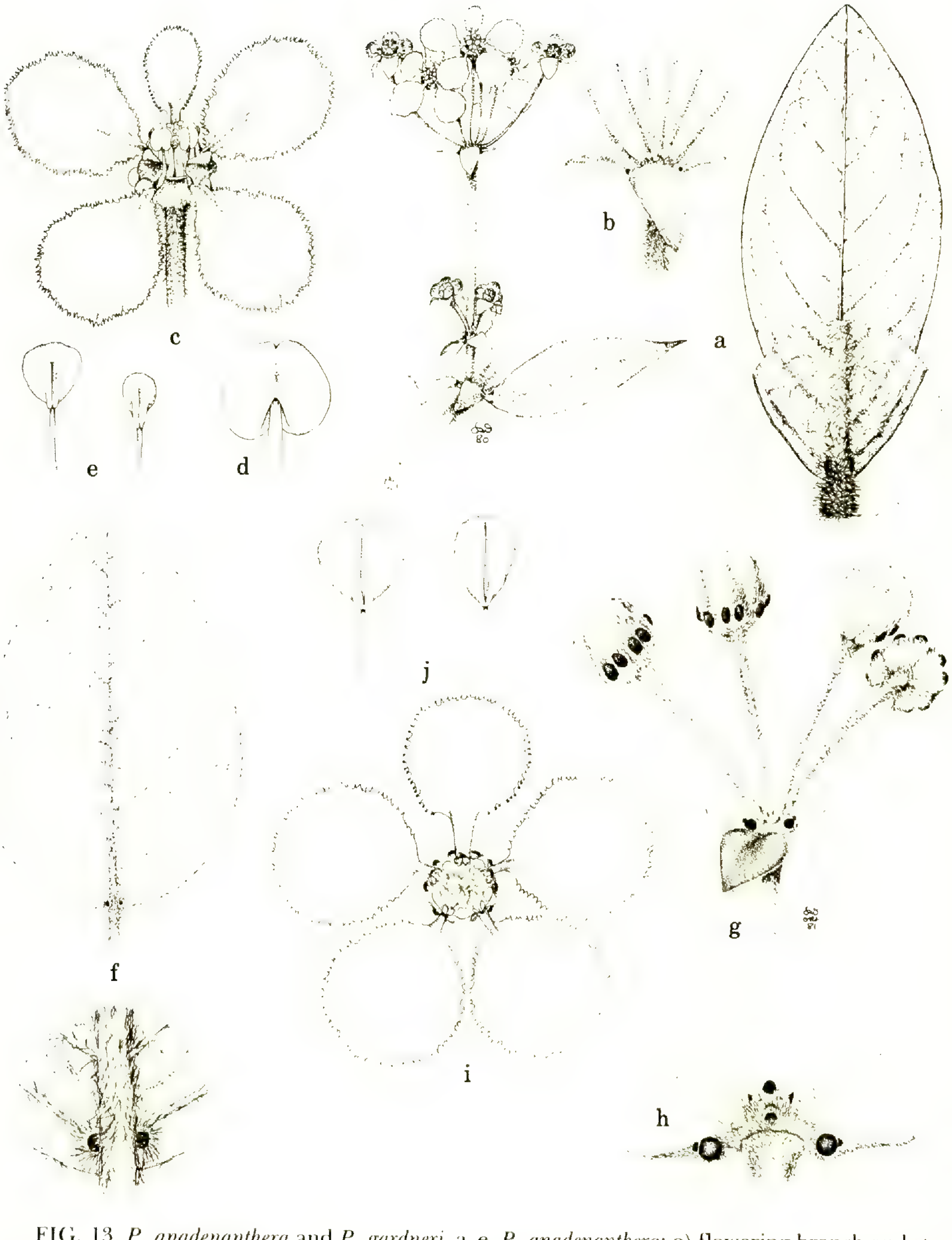

FIG. 13. *P. anadenanthera* and *P. gardneri*. a–e, *P. anadenanthera*: a) flowering branch and stem leaf, × 0.5, detail 2.5; b) base of a distal umbel, × 1.5; c) flower, × 1.75; d) abaxial view of anther, × 7.5; e)anterior (left) and posterior-lateral (right) staminode glands, × 7.5. f–j, *P. gardneri*: f) stem leaf, × 0.5, detail × 2.5; g) base of a distal umbel, × 1.5; h) terminal node with bases of secondary axes, all pedicels shed, × 2.5; i) flower, × 1.5; j) anterior (left) and posterior-lateral (right) staminode glands, × 7.5. a–e from *Hatschbach 36904*, f–j from *Gardner 3069 p.p.*

FIG. 14. *P. bahiana, P. andersonii* and *P. irwinii*. a–e, *P. bahiana*: a) flowering branch, × 0.5; b) base of a distal umbel, × 1.5; c) posterior (above) and anterior-lateral (below) petals, × 3; d) posterior-lateral (left) and anterior (right) staminodes, × 5; e) gynoecium, anterior style to right, × 5. f–i, *P. andersonii*: f) flowering branch and stem leaf, × 0.5; g) base of a distal umbel, × 1.5; h) flower, × 1.5; i) posterior-lateral (left) and anterior (right) staminodes, × 5. j–m, *P. irwinii*: j) stem leaf, × 0.5; k) base of a distal umbel, × 1.5; l) flower, × 1.5; m) anterior (above) and posterior-lateral (below) staminodes, × 5. a–e from *Irwin et al. 14889*, f–i from *Anderson 11591*, j–m from *Irwin et al. 28236b*.

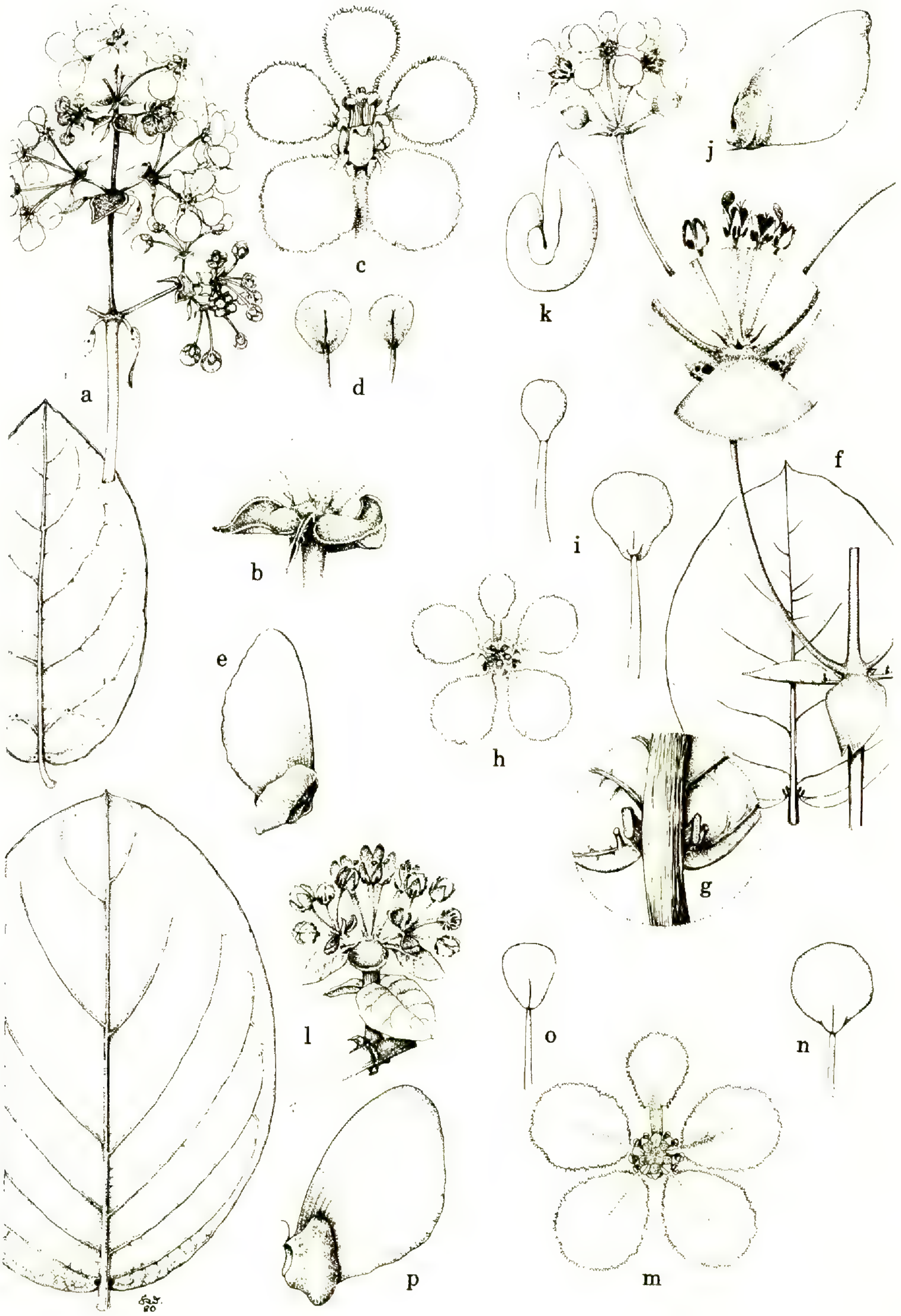

FIG. 15. *P. paludosa, P. hatschbachii* and *P. axillaris*. a–e, *P. paludosa*: a) flowering branch and stem leaf, × 0.5; b) base of a distal umbel, × 2.5; c) flower, × 1.5; d) anterior (left) and posterior-lateral (right) staminode glands, × 5; e) samara, × 0.75. f–k, *P. hatschbachii*: f) flowering branch and stem leaf, × 0.5, detail × 1.5; g) base of stem leaf, × 2.5; h) flower, × 1; i) posterior-lateral (above) and anterior (below) staminodes, × 7.5; j) samara, × 1; k) embryo, × ca. 5. l–p, *P. axillaris*: l) flowering shoot and stem leaf, × 0.5; m) flower, × 1; n) anterior staminode gland, × 7.5; o) posterior-lateral staminode gland, × 7.5; p) samara, × 1. a flowering branch from *Williams & Assis 6940*, leaf from *Barreto 8681*, b–d from *Williams & Assis 6940*, e from *Warming s.n.*, f–k from *Hatschbach 36675*, l–p from *Irwin & Soderstrom 7443*.

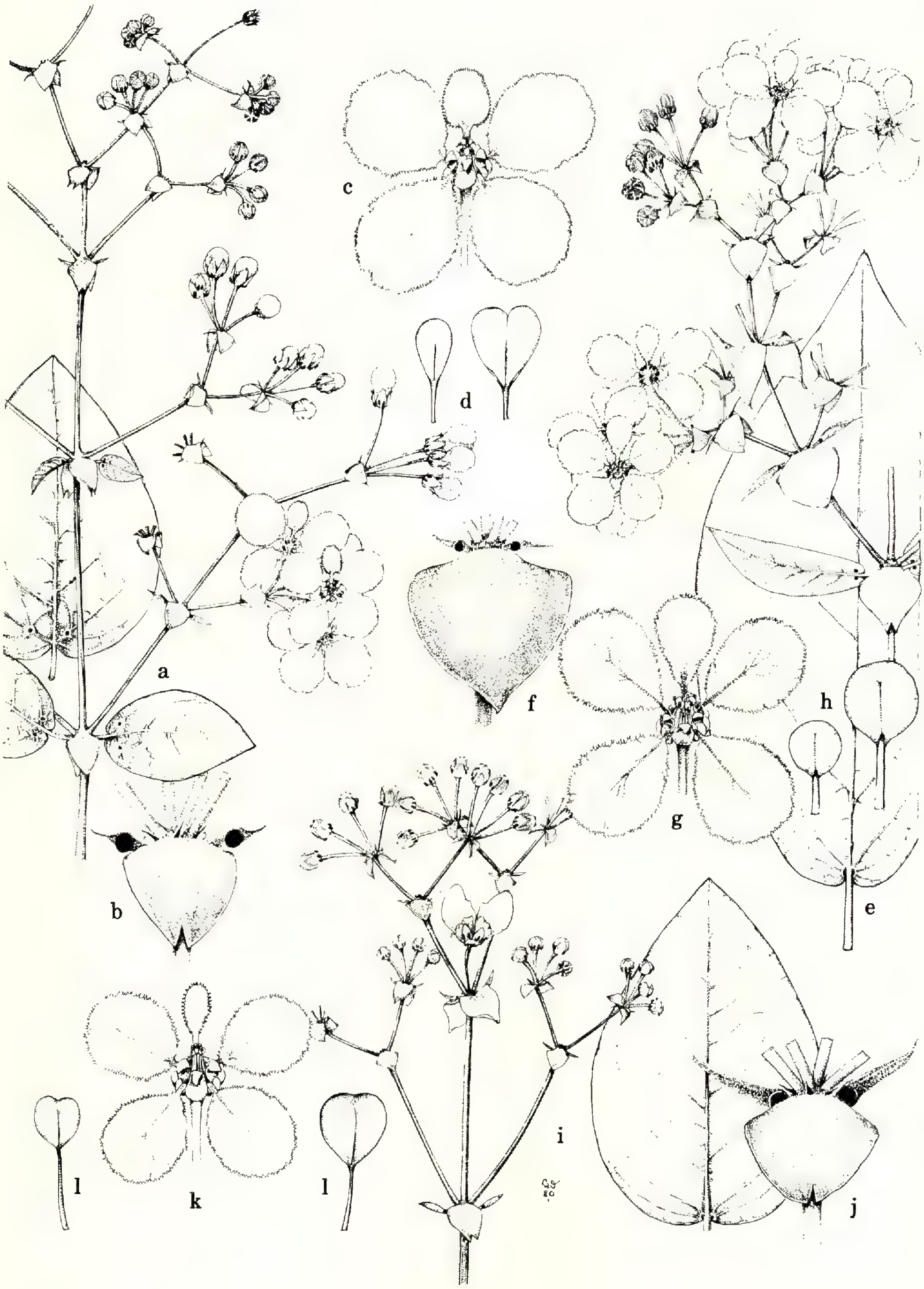

FIG. 16. *P. spinensis*, *P. leptoclada* and *P. barnebyi*. a–d, *P. spinensis*: a) flowering branch and stem leaf, × 0.5; b) base of a distal umbel, × 2.5; c) flower, × 1; d) posterior-lateral (left) and anterior (right) staminode glands, × 7.5. e–h, *P. leptoclada*: e) flowering branch and stem leaf, × 0.5; f) base of a distal umbel, × 2.5; g) flower, × 1; h) posterior-lateral (left) and anterior (right) staminode glands, × 7.5. i–l, *P. barnebyi*: i) flowering branch and stem leaf, × 0.5; j) base of a distal umbel, × 2.5; k) flower, × 1; l) posterior-lateral (left) and anterior (right) staminode glands, × 7.5. a–d from *Anderson 8730*, e–h from *Pohl 2946*, i–l from *Anderson 8623*.

FIG. 17. *P. catarinensis*, *P. glabra* and *P. hispidula*. a–e, *P. catarinensis*: a) flowering branch and stem leaf, × 0.5, detail × 2.5; b) base of a distal umbel, × 1.5; c) androecium and gynoecium, claw of posterior petal, × 3.5; d) anterior (left) and posterior-lateral (right) staminodes, × 7.5; e) samara, × 1. f–j, *P. glabra*: f) flowering branch, × 0.5, detail × 2.5; g) base of a distal umbel, × 1.5; h) flower, × 1.5; i) posterior-lateral (above) and anterior (below) staminode glands, × 7.5; j) samara, × 1. k–o, *P. hispidula*: k) stem leaf, × 0.5, detail × 2.5; l) flowering branch, × 0.5; m) claw of posterior petal, androecium opened out, with 1 posterior-lateral and 1 anterior-lateral stamen and 1 anterior-lateral staminode removed, × 3.5; n) anterior (above) and posterior-lateral (below) staminode glands, × 7.5; o) samara, × 1. a branch from *Smith & Reitz 12276*, leaf from *Reitz 3240*, b–e from *Smith & Reitz 12276*, f–i from *Irwin et al. 28371*, j from *Irwin et al. 28412*, k–n from *Harley et al. 18510*, o from *Araujo 140*.

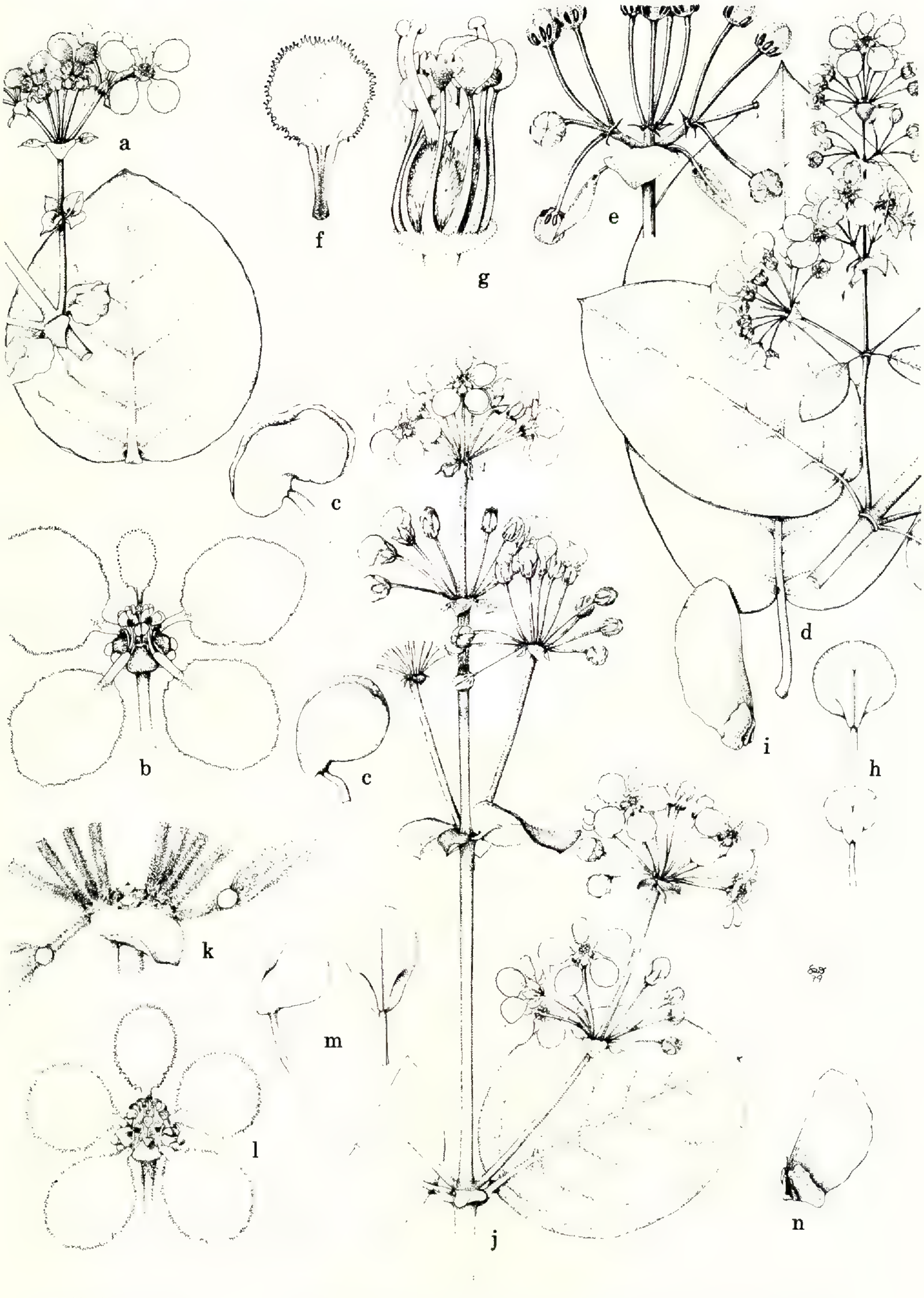

FIG. 18. *P. cipoana*, *P. parviflora* and *P. tomentosa*. a–c, *P. cipoana*: a) flowering branch and stem leaf, × 0.5; b) flower, × 1.5; c) anterior (above) and posterior-lateral (below) staminode glands, × 10. d–i, *P. parviflora*: d) flowering branch and stem leaf, × 0.5; e) base of a distal umbel, × 1.5; f) posterior petal, × 3.5; g) androecium and gynoecium, with posterior styles to left, × 7.5; h) anterior (above) and posterior-lateral (below) staminode glands, × 10; i) samara, × 0.75. j–n, *P. tomentosa*: j) flowering branch, × 0.5; k) base of a distal umbel, × 2.5; l) flower, × 1.5; m) posterior-lateral (left) and anterior (right) staminode glands, × 10; n) samara, × 0.75. a from *Atala 62*, b, c from *Vidal R108249*, d flowering branch from *Dusén 9225*, leaf from *Widgren s.n.*, e from *Glaziou 10371*, f–h from *Sucre 7560*, i from *Widgren s.n.*, j from *Langsdorff s.n.*, k from *Irwin et al. 28236a*, l, m, from *Eiten & Eiten 11072*, n from *Maguire 44770*.

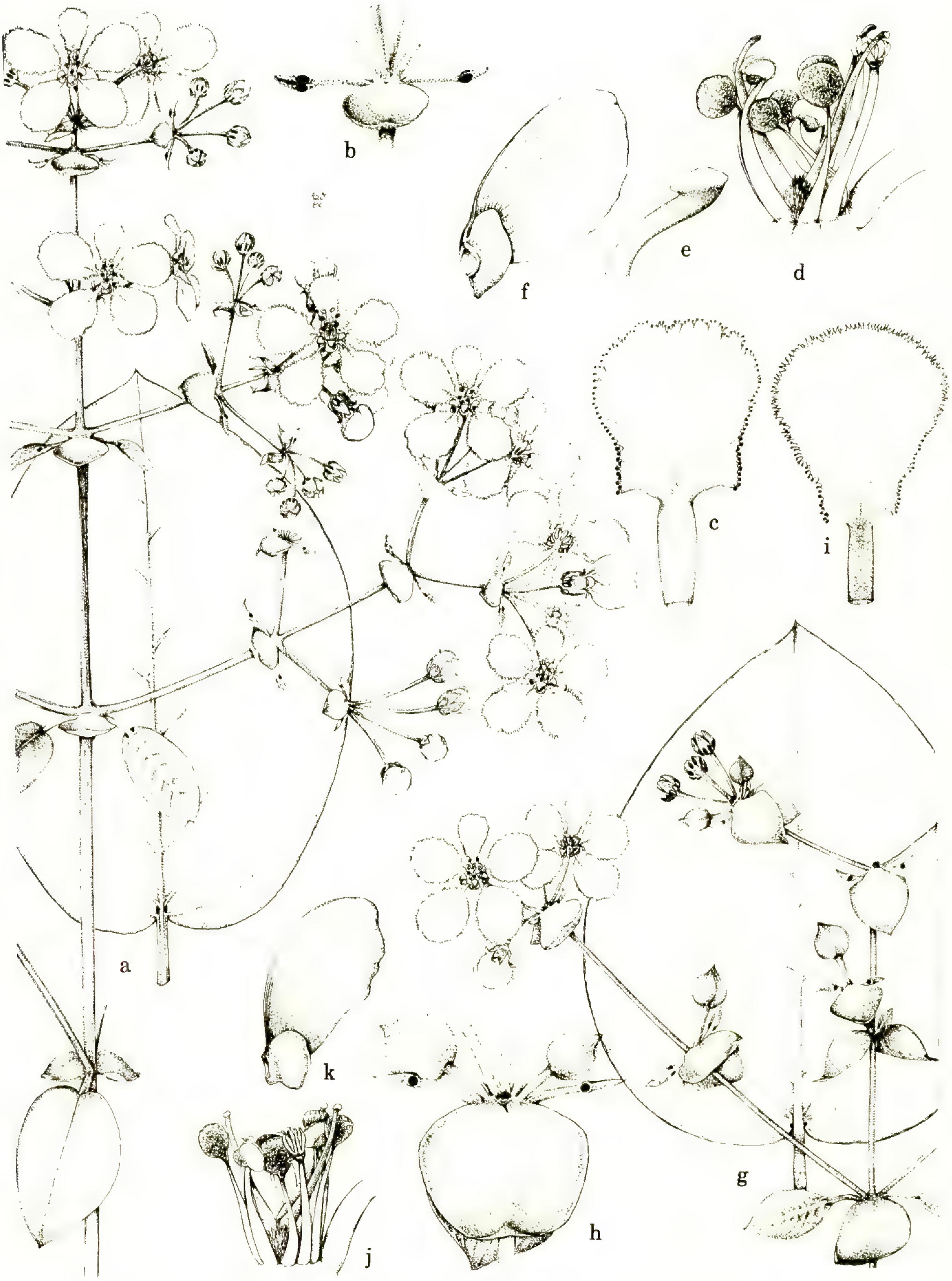

FIG. 19. *P. magnifica* and *P. cordistipula*. a–f, *P. magnifica*: a) flowering branch and stem leaf, × 0.5; b) base of a distal umbel, × 1.5; c) posterior petal, × 2.5; d) androecium and gynoecium, claw of posterior petal, × 3; e) stigma of anterior style, × 15; f) samara, × 0.75. g–k, *P. cordistipula*: g) flowering branch and stem leaf, × 0.5; h) base of a distal umbel, × 1.5; i) posterior petal, × 2.5; j) androecium and gynoecium, claw of posterior petal, × 3; k) samara, × 0.75. a, b from *Anderson 9831*, c–e from *Anderson 9474*, f from *Irwin et al. 17631*, g branch from *Lindman A3533*, leaf from *Malme 1919*, h–j from *Lindman A3533*, k from *Kuntze s.n.*

FIG. 20. *P. goiana* and *P. hirta*. a–h, *P. goiana*: a) flowering branch and stem leaf, × 0.5; b) base of a distal umbel, × 2.5; c) flower, × 1.5; d) posterior petal, × 1.5; e) anterior (above) and posterior-lateral (below) staminode glands, × 10; f) gynoecium, anterior style to left, × 5; g, h) samaras, × 1. i–m, *P. hirta*: i) stem leaf, × 0.5; j) base of stem leaf, × 2.5; k) base of a distal umbel, × 2.5; l) flower, × 1.5; m) anterior (above) and posterior-lateral (below) staminodes, × 10. a branch from *Irwin et al. 18616*, leaf from *Irwin et al. 34601*, b–c, e–f from *Irwin et al. 18616*, d from *Anderson 6201*, g from *Lima et al. 5*, h from *Irwin et al. 12351*, i–m from *Martius s.n.*

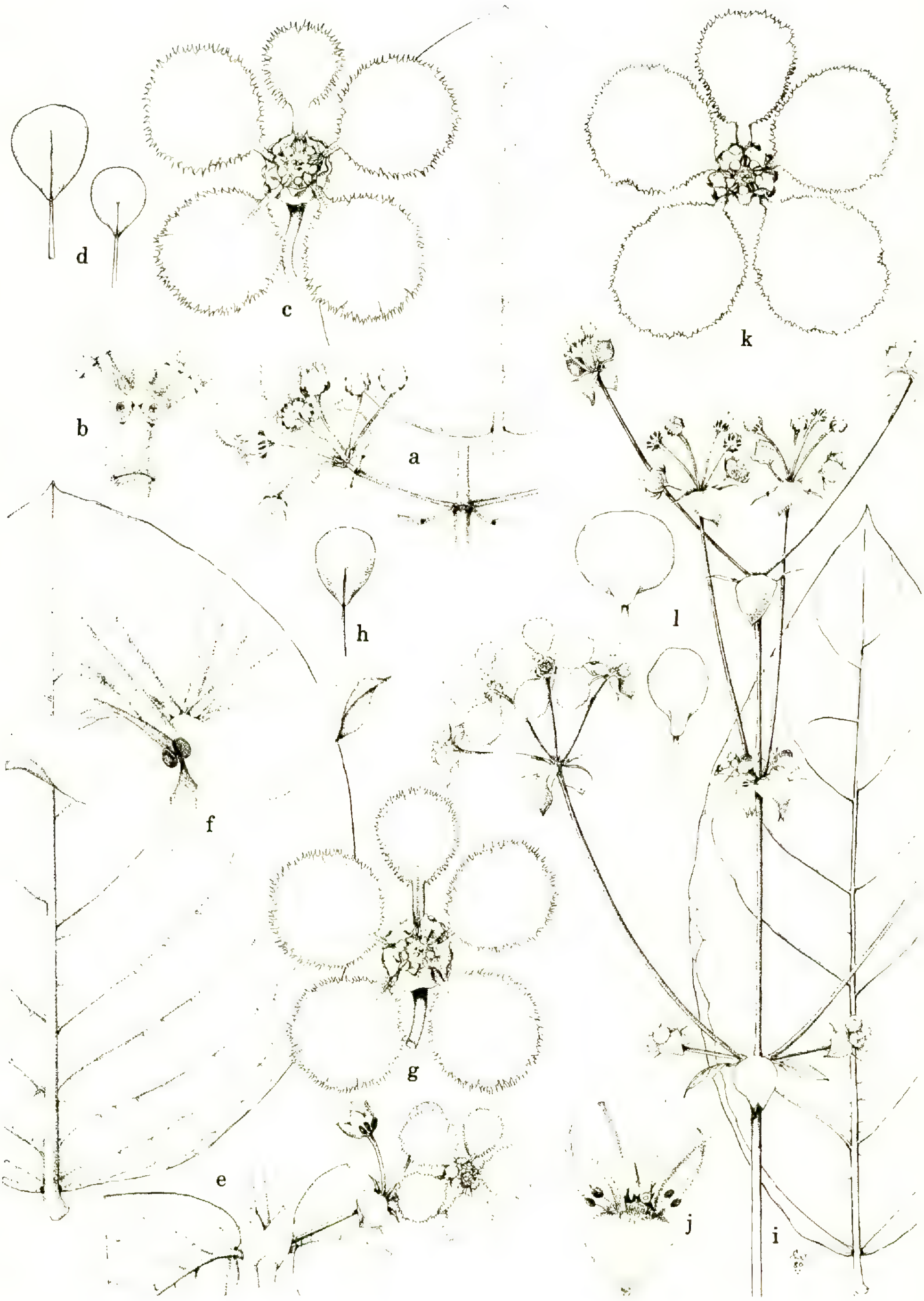

FIG. 21. *P. octoflora*, *P. megalantha* and *P. psilophylla*. a–d, *P. octoflora*: a) flowering branch and stem leaf, × 0.5; b) base of distal umbel (with 2 flowers removed), × 2; c) flower, × 1; d) anterior (left) and posterior-lateral (right) staminode glands, × 7.5. e–h, *P. megalantha*: e) flowering branch and stem leaf, × 0.5; f) base of a distal umbel, × 2; g) flower, × 1; h) anterior staminode gland, × 7.5. i–l, *P. psilophylla*: i) flowering branch and stem leaf, × 0.5; j) base of a distal umbel, × 2; k) flower, × 1.5; l) anterior (above) and posterior-lateral (below) staminode glands, × 7.5. a–d from *Irwin et al. 16681a*, e–h from *Anderson et al. 36870*, i branch from *Irwin et al. 16778*, leaf from *Sick B481*, j from *Irwin et al. 16778*, k, l from *Irwin et al. 16860*.

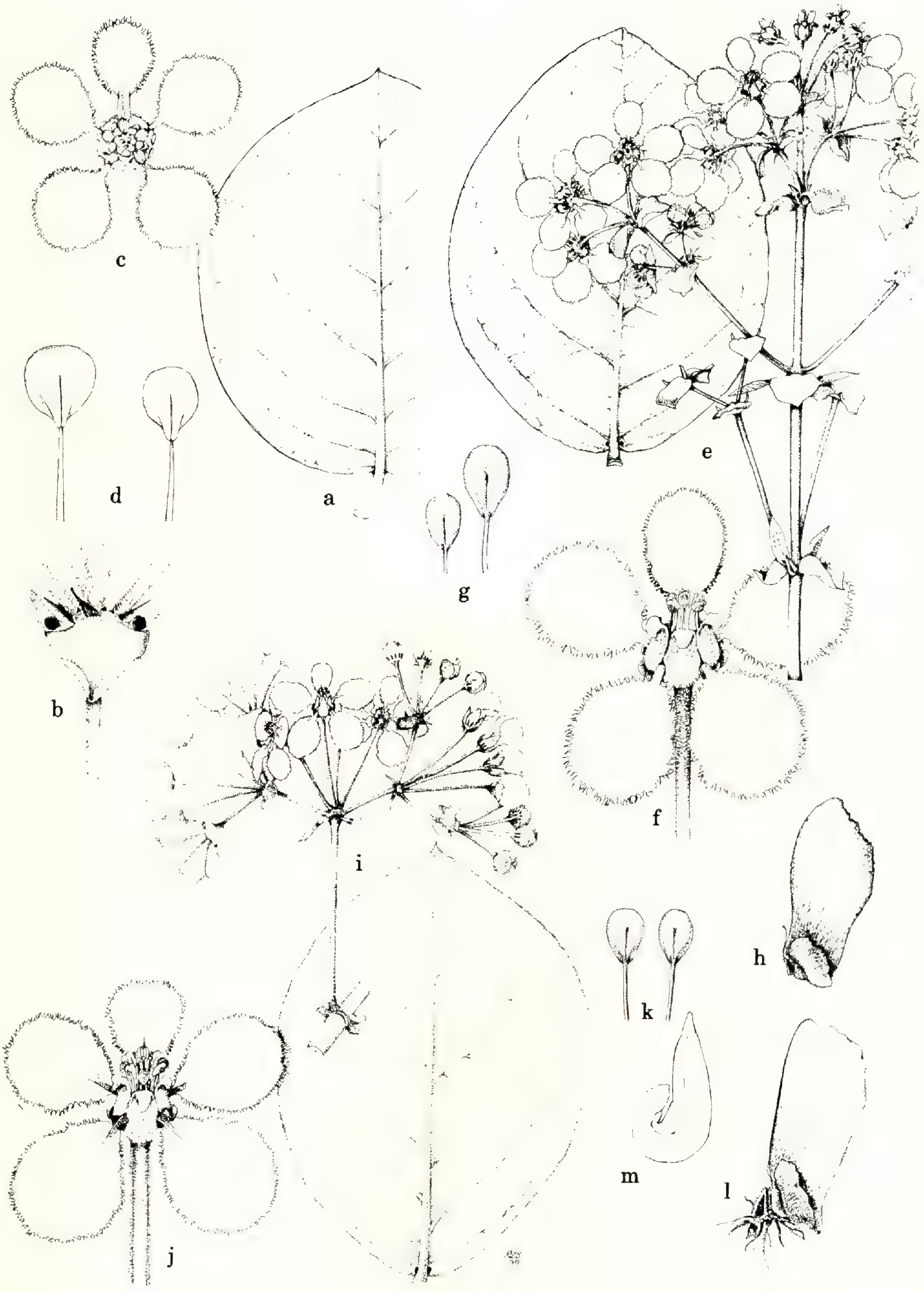

FIG. 22. *P. reticulata*. a–d, from east-central Mato Grosso: a) stem leaf, × 0.5; b) base of a distal umbel, × 2; c) flower, × 1; d) anterior (left) and posterior-lateral (right) staminodes, × 7.5. e–h, from Minas Gerais: e) flowering branch and stem leaf, × 0.5; f) flower, × 1.5; g) posterior-lateral (left) and anterior (right) staminode glands, × 5; h) samara, × 0.75; i–m, from São Paulo: i) flowering branch and stem leaf, × 0.5; j) flower, × 1.5; k) anterior (left) and posterior-lateral (right) staminode glands, × 5; l) samara on torus, × 0.75; m) embryo, × 3.5. a–d from *Irwin et al. 16681b*, e branch from *Mexia 5798*, leaf from *Brade 14819*, f–h from *Mexia 5798*, i from *Eiten & Eiten 3291*, j, k from *Eiten & Eiten 2914*, l m, from *Eiten & Eiten 2928*.

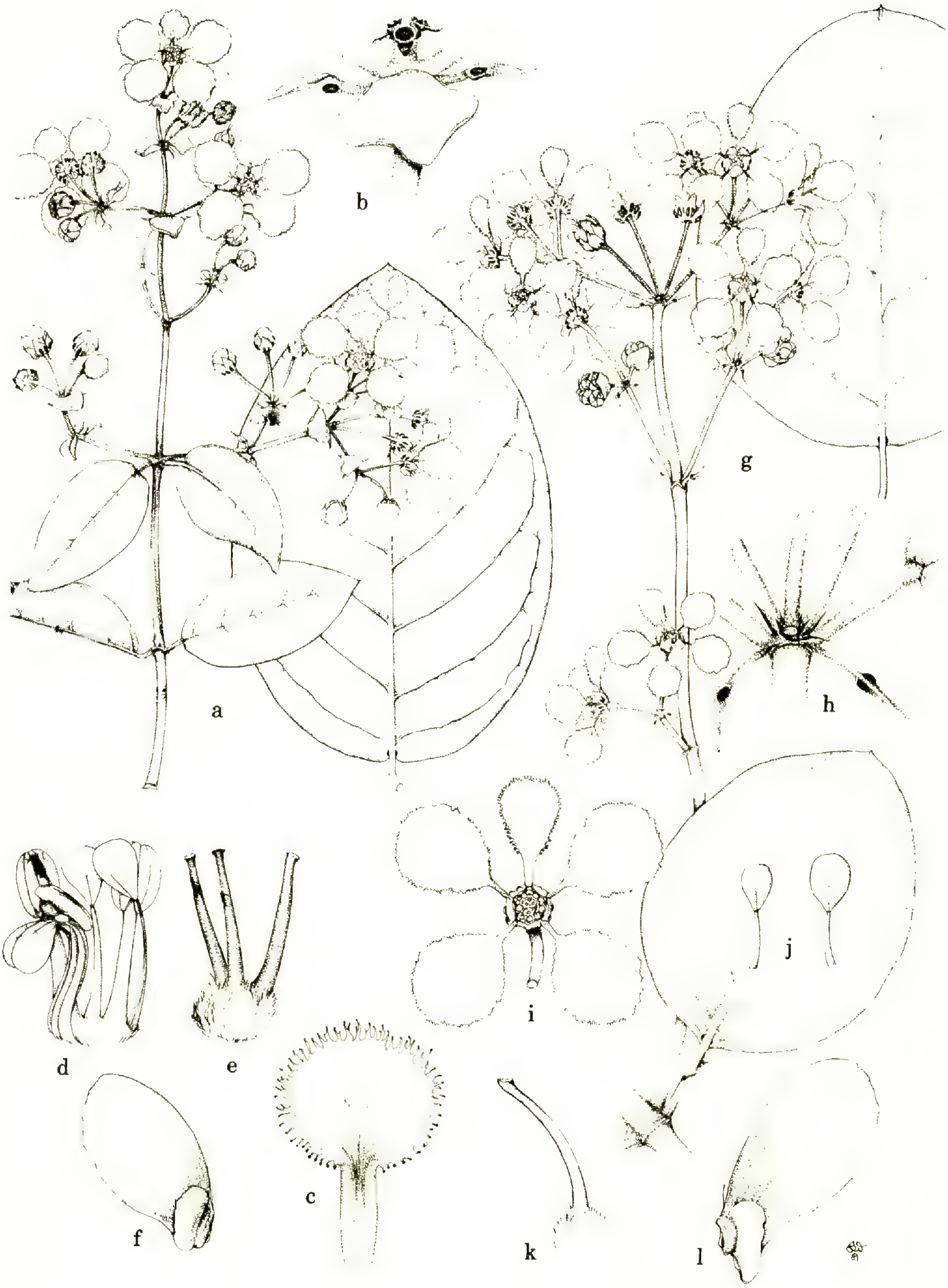

FIG. 23. *P. reticulata*. a–f, from Paraguay: a) flowering branch and stem leaf, × 0.5; b) base of a distal umbel, × 2.5; c) posterior petal, × 2.5; d) androecium (posterior-lateral stamen and anterior-lateral staminode and stamen removed), × 5; e) gynoecium, anterior style to right, × 5; f) samara, × 0.75. g–l, from southern Mato Grosso: g) flowering shoot and stem leaf, × 0.5; h) base of a distal umbel, × 2.5; i) flower, × 1; j) posterior-lateral (left) and anterior (right) staminode glands, × 5; k) anterior carpel, × 5; l samara, × 0.75. a branch from *Hassler 8166*, leaf from *Hassler 4055*, b–e from *Hassler 8166*, f from *Hassler 9881a*, g–l from *Hatschbach 24625*.

Contr. Univ. Mich. Herb. 15:93–136. 1982.

NOTES ON NEOTROPICAL MALPIGHIACEAE—I

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My current studies of American Malpighiaceae include both monographic and floristic projects, as well as routine identification of many specimens sent as gifts. In the course of this work I regularly encounter taxa new to science, situations in need of nomenclatural adjustment, and material that supplements our previous knowledge, such as flowering material of a species hitherto known only in fruit. It will be many years before I can complete and publish revisions for large difficult genera like *Byrsonima* and *Heteropterys*. These notes will serve as a vehicle for the earlier publication of miscellaneous descriptions and other observations as they accumulate.

BYRSONIMA

The species treated below are presented in approximately the order in which I believe they would have appeared in Niedenzu's monograph of the family (1928). This is done in order to facilitate their comparison and integration with that treatment.

Byrsonima hatschbachii W. R. Anderson, sp. nov. Fig. 1.

Suffrutex caulibus 23–40 cm altis plerumque non ramosis ex xylopodio enascentibus. Lamina foliorum majorum 11.5–16.5 cm longa, 1.4–1.6 cm lata, lineari-elliptica; petiolus 2–3 mm longus; stipulae 2–2.7 mm longae, basi connatae distaliter liberae. Inflorescentia bracteis bracteolisque persistentibus. Petala lutea; petalum posticum ungue eglanduloso. Antherae 2–2.5 mm longae, sparsim sericeae praecipue inter loculos, connectivo loculos ± aequanti. Ovarium glabrum.

Compact subshrub, with stems 23–40 cm tall, finely sericeous to glabrate, unbranched or nearly so, all arising from a xylopodium. Lamina of the larger leaves 11.5–16.5 cm long, 1.4–1.6 cm wide, linear-elliptical, very gradually tapered to an acute or acuminate apex and attenuate base, thinly sericeous to glabrate, with the short white hairs longest persistent on the adaxial midrib, the lateral veins prominulous on both sides; petiole 2–3 mm long, not clearly distinguishable from the lamina, sericeous to glabrate; stipules 2–2.7 mm long, connate only in the proximal third, the free portions triangular or acuminate, abaxially sericeous, adaxially glabrous. Inflorescence 9–11 cm long, finely sericeous with the hairs brown to gray, the flowers borne 1 per bract or (especially proximally) in compact cincinni of 2–3 flowers; bracts 2–4 mm long, 0.6–1 mm wide, subulate or narrowly triangular, thinly sericeous to glabrate, stiff; primary floriferous peduncle (from bract to joint) 0–3 mm long, developed only at lower nodes; bracteoles like the bracts but shorter; bracts and bracteoles

FIG. 1. *Byrsonima hatschbachii* and *B. affinis*. a–f, *B. hatschbachii*: a) habit, × 0.5; b) intrapetiolar stipules, adaxial view, × 4; c) 2-flowered cincinnus, × 2.5; d) posterior petal, × 3.5; e) stamens, × 7.5; f) gynoecium, with styles bending away from posterior petal, × 7.5. g–l, *B. affinis*: g) flowering branch, × 0.5, with abaxial lamina × 2.5 in circle; h) stipules, × 1.5; i) 2-flowered cincinnus, × 1.5; j) stamens, × 5; k) gynoecium, with styles bending away from posterior petal, × 5; l) fruit, × 0.5. Drawn by Karin Douthit, a–f from *Hatschbach 37593*, g–k from *Anderson 11274*, l from *Anderson 9518*.

persistent at least past flowering. Pedicel 4.5–6 mm long in flower, sericeous, circinate in bud, decurved in old flowers. Flower 12–13 mm in diameter. Sepals all biglandular, ca 1.5–2 mm long beyond the glands, 1.5 mm wide, obtuse, abaxially sericeous in center, ciliate on margin, adaxially glabrous, recurved at the apex in anthesis; glands 1–2.5 mm long. Petals yellow, glabrous; lateral petals reflexed, with the claw ca 2.5 mm long, the limb 4.5–5 mm long, 5–6 mm wide; posterior petal with the claw 2.5 mm long, erect, eglandular, the limb 4 mm long and wide, reflexed. Filaments 1.9 mm long, abaxially glabrous, adaxially hirsute at the base; anthers 2–2.5 mm long, sparsely sericeous, especially between the locules, the locules unwinged, often free at the apex, the connective not or hardly exceeding the locules. Ovary 1.3 mm high, glabrous, all 3 locules fertile; styles 3 mm long, distally slightly bent away from the posterior petal. Fruit unknown.

TYPE: BRAZIL. Mato Grosso: Mun. Chapada dos Guimarães, Capão Seco, campo cerrado, borda das depressões úmidas, 15 Nov 1975 fl, *Hatschbach 37593* (MBM, holotype; MICH, isotype).

Byrsonima hatschbachii is named in honor of Gert Hatschbach, a fine botanist whose "olho vivo" seldom misses a novel plant. The species seems to be most closely related to *B. intermedia* Adr. Juss., from which it differs in its short, nearly unbranched stems, long narrow leaves, nearly distinct stipules, and persistent bracts and bracteoles. *B. intermedia* is rather variable and as presently defined may well comprise more than one species. However, even in its broadest interpretation it could not accommodate *Hatschbach 37593*, nor have I seen any specimens intermediate between the two species.

Byrsonima morii W. R. Anderson, sp. nov. Fig. 7.

Frutex 1.5–2 m altus. Lamina foliorum majorum (5–) 6–8.2 cm longa, (3–) 4–6.1 cm lata, late elliptica vel parum ovata obovatave vel fere orbicularis, coriacea, subtus pertinaciter sericea vel appresso-tomentosa vel glabrescens, reticulo plerumque stramineo et prominenti, praecipue in pagina adaxiali; petiolus (3–) 5–12 (–15) mm longus; stipulae (1.5–) 2–3 mm longae, omnino connatae. Inflorescentia (4–) 6–9 (–13) cm longa, floribus in dimidio distali congestis, bracteis bracteolisque demum deciduis. Petala lateralia alba, petalum posticum flavum. Antherae 2–2.9 mm longae, glabrae vel sparsim sericeae inter loculos, connectivo loculos ± aequanti. Ovarium glabrum.

Shrub 1.5–2 m tall, the stems sericeous, the short hairs brown and persistent in the first season of growth, turning white and eventually deciduous in later seasons. Lamina of the larger leaves (5–) 6–8.2 cm long, (3–) 4–6.1 cm wide, broadly elliptical or slightly ovate or obovate to nearly orbicular, obtuse, rounded, or emarginate at the apex, slightly revolute at the margin, cuneate or truncate and shortly decurrent at the base, coriaceous, often glaucous above, sericeous or appressed-tomentose, persistently so or early or eventually glabrescent, the hairs above rather twisted and soon turning white, the hairs below nearly straight to serpentine or moderately twisted, reddish or sometimes eventually turning white, the lateral veins and reticulum usually yellowish and prominent, especially above; petiole (3–) 5–12 (–15) mm long, subsericeous to glabrescent; stipules (1.5–) 2–3 mm long, rounded, smoothly and completely connate, abaxially sericeous to glabrate, adaxially glabrous. Inflorescence (4–) 6–9 (–13) cm long, with flowers mostly densely clustered in the distal half, subsericeous proximally to nearly velutinous distally, the flowers borne mostly 1 per bract, occasionally in 2–flowered cincinni; bracts 1.5–3 mm long, 0.7–1.4 mm wide, triangular, stiff or reflexed apically, abaxially hairy, adaxially glabrous; peduncle 0–1 (–3) mm long; bracteoles like the bracts but smaller; bracts and

bracteoles persistent through anthesis, mostly deciduous before maturation of the fruit. Pedicel 7–12 mm long (–15 mm in fruit), reddish-tomentose, circinate in bud, decurved and eventually twisted in fruit. Flower 12–15 mm in diameter. Sepals all biglandular, 1.5–2.5 mm long beyond the glands, 1.8–2.5 mm wide, obtuse or rounded at the apex, abaxially loosely but densely sericeous, adaxially glabrous or sparsely tomentose distally, appressed but recurved at the apex in anthesis, accrescent (to 2–3 times as large) in fruit; glands 2–3 mm long. Petals glabrous, the lateral 4 white, the posterior bright yellow turning red-orange in age; lateral petals strongly reflexed, with the claw 3–3.5 mm long, the limb 4.3–6.5 mm long, 5.5–8 mm wide; posterior petal erect, with the claw 3–3.5 mm long, the limb 3.5 mm long, 4 mm wide, corrugated. Filaments 2–2.5 mm long, abaxially glabrous, adaxially hirsute at the base; anthers 2–2.9 mm long, glabrous or with a few long straight hairs between the locules, the locules unwinged, sometimes free at the apex, the connective not or hardly exceeding the locules (up to 0.3 mm). Ovary 1.4–1.7 mm tall, glabrous, all 3 locules fertile; styles 3–4 mm long, straight or bent at the apex. Mature fruit not seen.

TYPE: BRAZIL. Bahia: Mun. Mucugê (=Mucujê), 3 km S de Mucujê, campo rupestre, 1000 m, 22 Dec 1979 fl, *Mori & Benton 13158* (CEPEC, holotype; MICH, isotype).

PARATYPES: BRAZIL: Bahia: 10–15 km N of Mucugê on road to Andaraí, sandstone hillside with shallow soils and large bluffs of exposed rock, 1100 m, Feb fl, *Harley 18864* (MICH); Mun. Mucujê, 3 km S de Mucujê, campo rupestre, 1000 m, Jul fl, *Mori et al. 12609* (MICH, US); Mun. Mucujê, 10–12 km NW de Mucujê, campo rupestre, 1000 m, Jul fl, *Mori et al. 12667* (MICH, US); Mun. Lençois, 15 km NW of Lençois, campo rupestre, 900 m, Jun fl, *Mori & Boom 14282* (MICH), Jun fr, *Mori & Boom 14283* (MICH); Mun. Lençois, 5 km N of Lençois, campo rupestre, Jun fl, *Mori & Boom 14402* (MICH).

When I first saw this species, I identified it (*Harley 18864*) as "*Byrsonima bumeliifolia* Adr. Juss. vel aff." However, since seeing the type of *B. bumeliifolia* in Paris I have changed my opinion. That type has very dense, tightly twisted, persistent hairs on the abaxial side of the lamina, as in *B. variabilis* Adr. Juss., and it seems likely that those two species are closely related, perhaps even conspecific. *B. morii* is more probably related to *B. brachybotrya* Nied., a species of Paraná and Santa Catarina. They have similar flowers crowded in short pseudoracemes, although these are longer and bear more flowers in *B. morii*. *B. morii* has the lamina much larger, especially wider (two or three times as wide) and borne on a longer petiole. The two also differ dramatically in their habit. *B. morii* is a shrub 1.5–2 m tall, while *B. brachybotrya* is a subshrub with slender branches 15–50 cm high from a woody, more or less subterranean, base.

Byrsonima morii honors Scott A. Mori, a fine botanist whose collections from southern Bahia comprise a major contribution to our knowledge of that flora.

Byrsonima onishiana W. R. Anderson, sp. nov. Fig. 2.

Suffrutex caulibus erectis usque ad 30 cm altis. Lamina foliorum majorum 10–17 cm longa, 1.5–3.5 cm lata, anguste oblonga vel obovata, apice acuta vel obtusa, basi attenuata; petiolus 5–12 mm longus; stipulae 2–3 mm longae, liberae vel usque ad ⅔ connatae. Inflorescentia bracteis bracteolisque persistentibus. Petala pallide rosea. Antherae 2.1–2.7 mm longae, glabrae vel sparsim sericeae inter loculos, connectivo loculos ± aequanti. Ovarium glabrum. Fructus 9–11 mm diametro.

Subshrub, the leafy stems erect, slender, up to 30 cm tall, arising from a thicker prostrate (?) underground (?) stem, loosely sericeous to glabrate. Lamina of the larger leaves 10–17 cm long, 1.5–3.5 cm wide, narrowly oblong or obo-

FIG. 2. *Byrsonima onishiana* and *B. spinensis*. a–f, *B. onishiana*: a) habit, including underground base, × 0.5; b) stipules, × 3.5; c) flower, × 2.5; d) stamens, × 7.5; e) gynoecium, with styles bending away from posterior petal, × 5; f) fruit, drawn from behind to show enlarged sepals and persistent petals, × 2. g–l, *B. spinensis*: g) flowering branch, × 0.5; h) stipules, × 5; i) cincinnus, × 2.5; j) stamens, × 7.5; k) gynoecium, × 5; l) enlarging fruit, × 2.5. Drawn by Karin Douthit, a–f from *Irwin et al. 25824*, g–l from *Anderson et al. 35339*.

vate, acute or obtuse at the apex, very gradually attenuate at the base, thinly appressed-tomentose to glabrescent, the lateral veins and reticulum prominulous on both sides but more strongly so above; petiole 5–12 mm long, distinguishable only with difficulty from the decurrent lamina, appressed-tomentose to glabrate, swollen at the base; stipules 2–3 mm long, triangular or ovate, distinct or connate for up to ⅔ of their length, abaxially loosely sericeous, adaxially glabrous. Inflorescence 3–13 cm long, loosely sericeous, the flowers borne 1 (–2) per bract; bracts 2–3 mm long (–8 mm at lowest flowers), 1–1.3 mm wide, narrowly triangular to subulate, stiff and ascending or spreading or somewhat recurved; peduncle none; bracteoles like the bracts but smaller; bracts and bracteoles persistent past maturity of the fruit. Pedicel 5–10 mm long or longer in fruit, loosely sericeous, circinate in bud, decurved and eventually twisted in fruit. Flower ca 14 mm in diameter. Sepals all biglandular, 1.5–2.5 mm long beyond the glands, 1.7–2.3 mm wide, obtuse at the apex, abaxially loosely sericeous, adaxially glabrous, recurved at the apex in anthesis, accrescent (to ca 3 times as large) in fruit; glands 1.7–2.3 mm long. Petals "very pale pink," glabrous; lateral petals reflexed, with the claw 2–3 mm long, the limb 5–5.5 mm long, 5.5–7 mm wide; posterior petal erect, with the claw 2.5 mm long, the limb 3.7 mm long, 4.5 mm wide, corrugated. Filaments 2–2.5 mm long, abaxially glabrous, adaxially hirsute at the base; anthers 2.1–2.7 mm long, glabrous or with a few long, straight hairs on inner faces of locules, the locules unwinged, often free at the apex, the connective not or hardly exceeding the locules (up to 0.2 mm). Ovary 1.2–1.6 mm high, glabrous, all 3 locules fertile; styles 3.6–3.8 mm long, straight or bent away from posterior petal at apex. Fruit 9–11 mm in diameter, glabrous; petals sometimes persistent nearly to maturity of fruit.

TYPE: BRAZIL. Minas Gerais: Serra dos Óculos, campo, ca 60 km NE of Patrocínio, 1050 m, 1 Feb 1970 fl/fr, *Irwin et al. 25824* (UB, holotype; MICH, NY, isotypes).

PARATYPE: BRAZIL. Verusa (without further locality data), Oct fl, *Heringer 10701* (UB).

Byrsonima onishiana is named in honor of Eunice Onishi, Brazilian botanist and one of the collectors of the type. It is most closely related to *B. oxyphylla* Adr. Juss., which has a similar habit and generally similar flowers. In *B. oxyphylla* the leaves are smaller (seldom over 6 cm long and 1.5 cm wide) and more numerous on each stem; its inflorescence is shorter and more congested, often almost umbellate; its petals are white (the lateral four) and yellow (the posterior one, turning red in age); and the drupe is smaller, 5–6 mm in diameter.

Byrsonima cacaophila W. R. Anderson, sp. nov. Fig. 3.

Arbor 10–20 m alta. Lamina foliorum majorum 13–24 cm longa, 5.5–10 cm lata, glabrata vel in costa pertinaciter sericea; petiolus 12–32 mm longus; stipulae 3.5–6.5 mm longae, omnino connatae vel distaliter distinctae. Inflorescentia cincinnis 1–3-floris, bracteis plerumque 3–5.5 mm longis, subulatis, reflexis, pedunculo primario (2–) 4–10 mm longo, bracteolis 1–2 mm longis, ovatis, bracteis bracteolisque persistentibus. Sepala adaxialiter glabra. Petala alba, aetate rubescentia. Antherae 2.2–2.9 mm longae, sericeae praecipue inter loculos pilis fusiformibus 0.4–0.5 mm longis, connectivo loculos ± aequanti. Ovarium glabrum. Fructus (siccus) 11 mm longus, 15–18 mm diametro, depressus, nuce costata.

Tree 10–20 m tall, the trunk 25–35 cm in diameter, the stems sericeous, eventually glabrescent. Lamina of the larger leaves 13–24 cm long, 5.5–10 cm wide, acute or obtuse to rounded and often abruptly short-acuminate at the apex, slightly revolute at the margin, cuneate at the base, glabrate at maturity or

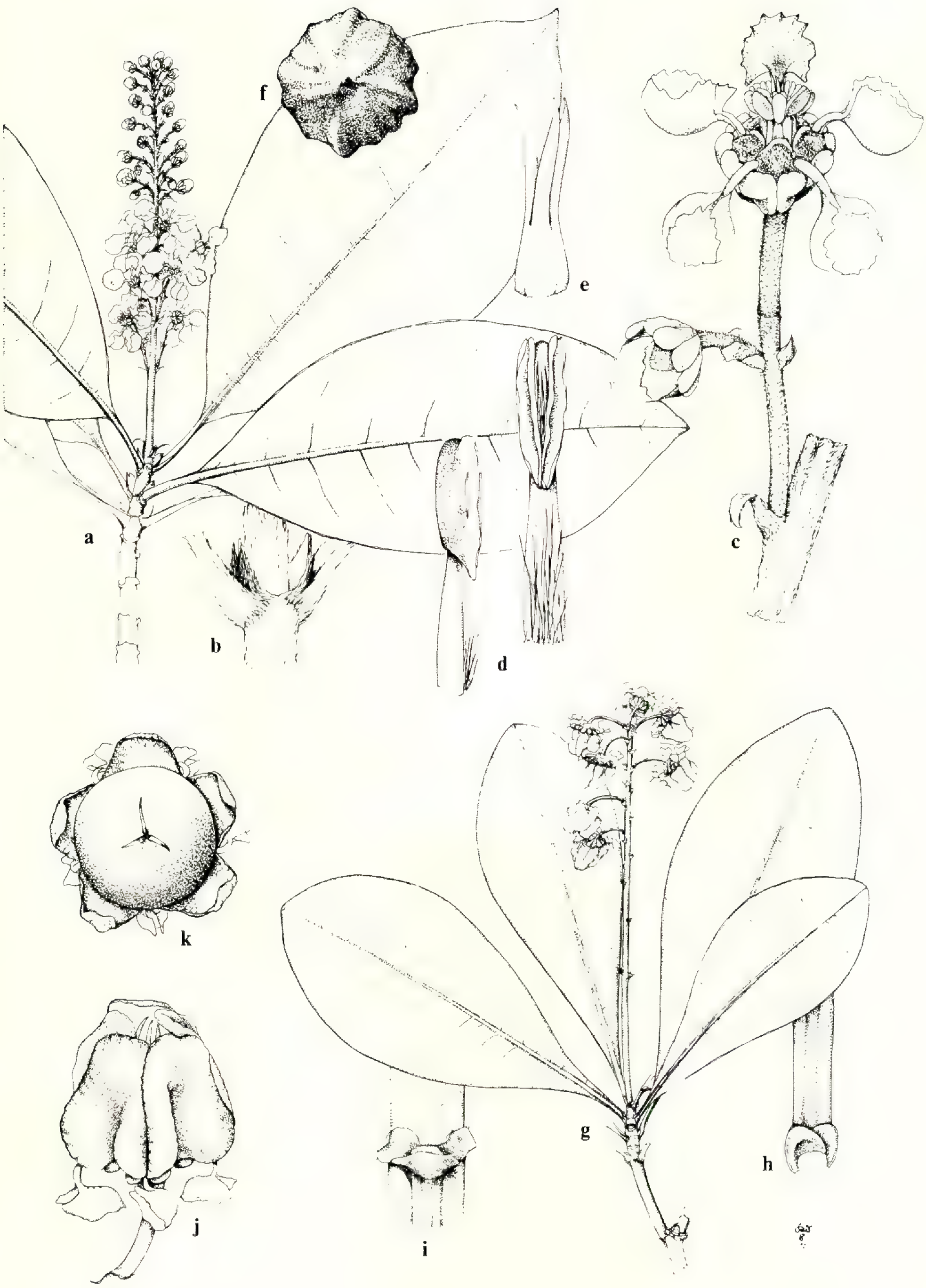

FIG. 3. *Byrsonima cacaophila* and *B. bahiana*. a–f, *B. cacaophila*: a) flowering branch, × 0.5; b) stipules, × 2; c) cincinnus, × 2.5; d) stamens, × 7.5; e) gynoecium, with anterior style to left, × 5; f) fruit (dried) from above, × 1. g–k, *B. bahiana*: g) fruiting branch, × 0.5; h) stipules, adaxial view, × 2.5; i) bract and bracteoles on inflorescence axis, × 5; j) immature fruit with enlarged sepals and persistent petals, × 2; k) fruit from above, × 1.3. Drawn by Karin Douthit, a–e from *Belém & Pinheiro 2881*, f from *Belém & Magalhães 637*, g–k from *Harley 18475*.

persistently sericeous on the midrib or rarely on the lateral veins below, the lateral veins prominent, especially below, the reticulum prominulous on both sides; petiole 12–32 mm long, sericeous to glabrate; stipules 3.5–6.5 mm long, triangular, completely connate or free distally, smooth or abaxially sulcate, abaxially sericeous to glabrescent, adaxially glabrous. Inflorescence (8–) 11–19 cm long, sericeous proximally to loosely sericeous to velutinous distally; cincinni with 1–3 flowers; bracts mostly 3–5.5 mm long, shorter at apex of inflorescence, 1–1.5 mm wide, subulate, mostly revolute at apex or reflexed or twisted, abaxially sericeous, adaxially glabrous; primary floriferous peduncle (from bract to first joint) (2–) 4–10 mm long; bracteoles 1–2 mm long, 1–1.5 mm wide, ovate, abaxially sericeous, adaxially glabrous, borne at or up to 2 mm below apex of peduncle; bracts and bracteoles persistent past maturity of the fruit. Pedicel 5–7 mm long, loosely sericeous to velutinous, slightly circinate in bud, apparently straight in fruit. Flower 17 mm in diameter. Sepals all biglandular, 2 mm long beyond the glands, 2–3 mm wide, acute or obtuse at the apex and revolute in anthesis, abaxially sericeous, adaxially glabrous; glands 3–4 mm long. Petals white, turning reddish in age, glabrous; lateral petals reflexed, with the claw 2.5–3 mm long, the limb 5–6 mm long, 6–7 mm wide, concave; posterior petal erect, the claw 3–3.8 mm long, eglandular, the limb 4–4.5 mm long, 5–6 mm wide, corrugated. Filaments 2.5–3 mm long, abaxially glabrous or sparsely hirsute at base, adaxially hirsute at base; anthers yellow, 2.2–2.9 mm long, the locules linear, unwinged, sericeous, especially on inner faces, with the fusiform hairs only 0.3–0.5 mm long, the connective equalling the locules or occasionally exceeding them by up to 0.2 mm. Ovary 1.5 mm high, conical, sulcate, glabrous, all 3 locules fertile; styles 3.5–4 mm long. Fruit (dried) 11 mm long, 15–18 mm in diameter, glabrous, depressed, the nut with prominent bony ribs.

TYPE: BRAZIL. Bahia: Rod. Uruçuca a Taboquinha, plantação de cacau, 22 Nov 1971 fl, *T. S. Santos 2200* (CEPEC, holotype; MICH, isotype).

PARATYPES: BRAZIL. Bahia: Centro de Pesquisas do Cacau, CEPLAC, Ilhéus, Apr fr, *Belém & Magalhães 637* (CEPEC, IAN, NY, UB); Itapebí plantação de cacau, Nov fl, *Belém & Pinheiro 2881* (CEPEC, NY, UB); Itajuípe, plantação de cacau, Nov fl, *Belém & Pinheiro 2918* (CEPEC, NY, UB); Itabuna, Estrada da Burarema, mata de cacau, Nov fl, *Mello Filho 2902/Emmerich 3440* (CEPEC, R); Ilhéus, CEPEC, plantação de cacau, Dec fl, *Santos 530* (CEPEC, MICH).

I am not sure where this interesting species fits best in the taxonomy of the genus. It resembles *B. maguirei* Anderson in its stipules, inflorescence, anther-shape, and sulcate ovary, but differs in having reflexed bracts, white petals, hairy anthers, and all three carpels fertile. The reflexed subulate bracts suggest the complex that includes *B. crispa* Adr. Juss., but *B. cacaophila* differs from those species in its long peduncles, white petals, persistent bracts and bracteoles, and short fusiform anther-hairs.

The epithet *cacaophila* draws attention to the fact that all kown collections of this species come from cacao plantations, including those from the CEPEC reserve, which was founded on an old plantation. When the native forests were cut many years ago to plant *Theobroma,* some native trees were left to shade the cacao trees. *Byrsonima cacaophila* seems to be one of those regularly spared; the species may owe its persistence to this practice. Many other undescribed species of those wonderful forests probably disappeared into extinction at that time.

According to the label with *Santos 2200,* this species has the common name "*Aca.*"

Byrsonima schunkei W. R. Anderson, sp. nov. Fig. 4.
Byrsonima poeppigiana Adr. Jussieu var. *velutina* Niedenzu in Engler, Pflanzenr. IV. 141: 715. 1928. Lectotype: *Tessmann 3450* (NY!).

Frutex vel arbor 2–10 m alta. Lamina foliorum majorum 20–29 cm longa, 8–14 cm lata, apice acuminata, supra mox glabrata praeter costam plerumque velutinam, subtus dense et pertinaciter velutina; petiolus (16–) 20–31 mm longus, velutinus; stipulae 4–8 (–10) mm longae, connatae, apice rotundatae. Inflorescentia bracteis 3–6 (–10) mm longis, 1.5–2.5 mm latis, cincinnis 1–4-floris, pedunculis primariis 3–15 mm longis, bracteolis 1.5–4 (–7) mm longis, 1.5–3 (–5) mm latis, sub apice pedunculi portatis. Sepala adaxialiter appresso-tomentosa. Petala lutea. Antherae 2.0–3.5 mm longae, laxe sericeae praecipue inter loculos, connectivo loculos aequanti vel usque 0.5 mm superanti et apice ut videtur glanduloso. Ovarium sericeum.

Shrub or tree 2–10 m tall; stems velutinous, eventually glabrescent. Lamina of the larger leaves 20–29 cm long, 8–14 cm wide, ellipical or broadly elliptical or somewhat obovate, cuneate at the base, slightly revolute at the margin, acuminate (sometimes aruptly so) at the apex, soon glabrate above except usually persistently velutinous on the midrib and sometimes on the lateral veins, densely and persistently velutinous below, the hairs 0.25–0.50 mm long, erect, bifurcate, the branches as long as or shorter than the stalk; midrib and lateral veins prominent below; petiole (16–) 20–31 mm long, velutinous like the lamina with a proximal admixture of some longer, sub-basifixed hairs; stipules 4–8 (–10) mm long, connate, the pair rounded at the apex, abaxially loosely sericeous, adaxially glabrous. Inflorescence 6–24 cm long, velutinous; cincinni comprising 1–4 flowers, often better developed proximally than distally in the same inflorescence; bracts 3–6 (–10) mm long, 1.5–2.5 mm wide, subulate, lanceolate, or ovate, stiffly spreading or somewhat flexuous distally, abaxially sericeous, adaxially glabrous; primary floriferous peduncle (from bract to first joint) 3–15 mm long; bracteoles 1.5–4 (–7) mm long, 1.5–3 (–5) mm wide, ovate, borne at various heights on peduncle from just above base to somewhat below apex; bracts and bracteoles deciduous during or after anthesis, all gone before maturation of the fruit. Pedicel 4–8 mm long, velutinous, circinate in bud, decurved or twisted in fruit. Flower ca 13 mm in diameter. Sepals all biglandular, 2–3 mm long beyond the glands, rounded at the apex, revolute, appressed-tomentose, densely so abaxially, densely to sparsely so adaxially, accrescent in fruit; glands 2.5–4.5 mm long. Petals yellow, glabrous, the outermost covering all others in bud; lateral petals reflexed, with the claw 2.5–3 mm long, the limb 5.5–6.5 mm long, 6–8 mm wide, concave, especially in the anterior pair; posteror petal erect, the claw 3–4 mm long and thicker, eglandular, the limb 3–4 mm long, 3.5–4.5 mm wide, corrugated. Filaments 2.0–2.5 mm long, adaxially hirsute at very base with hairs only ca 0.5 mm long; anthers 2.0–3.5 mm long, loosely sericeous, especially between the locules, the connective equalling the locules or exceeding them by up to 0.5 mm and apparently glandular at the apex, the locules narrowly linear, separated on the connective, free at the apex. Ovary 1.3–1.6 mm high, conical, sericeous, at least on the distal half, all 3 locules fertile; styles 3–3.5 mm long, straight or slightly bent at the apex. Fruit yellow, 13–15 mm long, 11–13 mm in diameter (dried), ovoid with an attenuate apex, glabrate or distally thinly sericeous.

TYPE: PERU. San Martín: Prov. Mariscal Caceres, Dtto. Tocache Nuevo, Apr fl, *Schunke V. 3929* (MICH, holotype).

PARATYPES: PERU. San Martín: Mariscal Caceres, Tocache Nuevo, Mar fr, *Gentry et al. 25569* (MICH), Jan fr, *Schunke V. 3699* (MICH), Nov fl, *Schunke V. 5589* (MICH), Aug fr, *Schunke V. 6859* (MICH, MO), Jul fl, *Schunke V. 7332*

FIG. 4. *Byrsonima schunkei* and *B. surinamensis*. a–f, *B. schunkei*: a) flowering branch and large leaf, × 0.5, with hair from abaxial side of lamina × 35; b) stipules, × 1.5; c) cincinnus, × 2.5; d) stamens, with long and short anthers from same flower, × 5; e) gynoecium, with styles bent away from posterior petal, × 5; f) fruit, × 1. g–l, *B. surinamensis*: g) flowering branch, × 0.5, with leaf-tip × 5; h) stipules, × 3.5; i) flower bud with bracts and bracteoles, × 2.5; j) stamens, with long and short anthers from same flower, × 7.5; k) gynoecium, × 7.5; l) fruit, drawn from behind to show enlarged sepals and twisted pedicel, × 1.5. Drawn by Karin Douthit, a–e from *Schunke 7332*, f from *Maas et al. P12974*, g–k from *Lindeman et al. 597*, l from *Mori & Bolten 8437*.

(MO, US); Uchiza, Pampa Yacu, alt. 450 m, Jan fl/imm. fr, *Schunke V. 5750* (F, LA). Loreto: Yarina cocha, middle Ucayali, Dec fl, *Tessmann 3450* (NY). Huánuco: Villa Isabel, río Cuchara, Sep fr, *Schunke V. 5676* (F, LA). BRAZIL. Acre: Mpio. Rio Branco, highway to Pôrto Velho, *Albuquerque et al. 1279* (MICH); Porangaba, Rio Juruá-mirim, May fr, *Maas et al. P12974* (MICH, NY); km 45 Rod. Rio Branco-Pôrto Velho, Feb imm. fr, *Santos et al. 53* (MICH). Amazônas: Antimary, Rio Acre, Mar fr, *Huber s.n.* (MG 4251). BOLIVIA. Pando: Cobija, Dec fl, *Ule 9488* (MG).

Byrsonima schunkei is named in honor of José Schunke Vigo, who has made several beautiful collections of it. The species grows in tall forest or, more often, in secondary forest or thickets, always on *terra firma*. Schunke has reported the following common names for the species in Peru: "Indana," "Indano," "Indano Colorado," and "Sacha Uvilla." He also records the following uses in folk-medicine: "La corteza la utilizan los nativos para curarse de tuberculosis, bebiendo en cocimiento" (*3929*). "A quarter of a glass of a maceration of the bark is drunk for dysentery" (*5750*).

Niedenzu described this species as *B. poeppigiana* var. *velutina*, but his concept of the taxon was vague and his syntypes included at least one collection referable to a third species, *B. linguifera*. I am selecting a lectotype for Niedenzu's name here, but nevertheless I feel it would be best to give the taxon a distinct epithet at the level of species. *Byrsonima schunkei* belongs to a complex of four species native to western Amazonia, which are closely related but easily distinguished. The following key will facilitate their recognition:

1. Leaves sericeous to glabrate below, the hairs sessile, straight, appressed. *B. arthropoda* Adr. Juss.
1. Leaves thinly to densely velutinous below, the persistent hairs Y-shaped with a straight, erect stalk, the branches mostly shorter than the stalk.
   2. Leaves strongly revolute and persistently velutinous above over entire surface of lamina. *B. linguifera* Cuatr.
   2. Leaves flat or only slightly revolute at the margin, soon glabrate above or persistently velutinous on the midrib.
      3. Floriferous peduncle 0.3–2 mm long (–3 mm in fruit); bracteoles borne at apex of peduncle, 0.8–1.5 (–2) mm long, 1 mm wide; larger leaves with the lamina 10–19 cm long and 4.5–9 cm wide, the petiole 6–15 (–18) mm long; sepals adaxially glabrous. *B. poeppigiana* Adr. Juss.
      3. Floriferous peduncle 3–15 mm long; bracteoles borne below apex of peduncle, 1.5–4 (–7) mm long, 1.5–3 (–5) mm wide; larger leaves with the lamina 20–29 cm long and 8–14 cm wide, the petiole (16–) 20–31 mm long; sepals adaxially sparsely to densely appressed-tomentose. *B. schunkei* Anderson

Byrsonima affinis W. R. Anderson, sp. nov. Fig. 1.

Arbor (3–) 4–8 (–10) m alta, trunco 30 cm diametro, torto, suberoso. Lamina foliorum undulata, margine revoluta, basi auriculata, sessilis, subtus arcte lanata, reticulo subtus prominenti. Inflorescentia bracteis 3–6 mm longis, 2.5–3.5 mm latis, anguste triangularibus, revolutis et/vel reflexis, bracteolis 1–2.5 mm longis, bracteis bracteolisque deciduis. Petala lutea; petalum posticum ungue eglanduloso. Antherae 2.5–3.5 mm longae, loculis glabris, connectivo extus plerumque laxe sericeo, inter loculos semper sericeo, loculos non vel usque ad 0.4 mm superanti. Ovarium lanatum. Fructus usque ad 3.7 cm diametro, luteus, nuce 12 mm alta, 18 mm lata, trilobata, basi excavata.

Tree (3–) 4–8 (–10) m tall; trunk up to 30 cm (or more?) in diameter, often twisted, with thick, fissured, corky bark; young stems tomentose with admixture of spreading hairs, soon glabrescent. Lamina of the larger leaves 11–20 cm long,

4–9 (–10) cm wide, elliptical or slighty obovate, acute, obtuse, or rounded at the apex, undulate, revolute at the margin, shallowly to deeply auriculate at the base, sessile, glabrate above except tomentose on the midrib, glaucous and smooth or somewhat rugose above, tightly and persistently woolly below, the hairs light brown or white, the lateral veins and reticulum very prominent below; petiole none; stipules 4–6 mm long, smoothly and completely connate or distinct at the apex, acute, abaxially tomentose or loosely sericeous, adaxially glabrous. Inflorescence 12–24 cm long, erect in flower and pendent in fruit, densely and persistently tomentose, the flowers borne 1 per bract or in clusters (compact cincinni) of 2 (–3?) flowers; bracts 3–6 mm long, 2.5–3.5 mm wide, narrowly triangular, abaxially tomentose, adaxially glabrous, mostly revolute and/or reflexed; peduncle 0; bracteoles smaller than the bracts, especially shorter (1–2.5 mm long), revolute or not; bracts and bracteoles deciduous, sometimes during anthesis, often later. Pedicel 8–15 mm long, thickened and slightly elongated in fruit, densely spreading-tomentose or velutinous, straight or slightly circinate in bud, often somewhat decurved after anthesis but apparently ± straight in mature fruit. Flower 18–22 mm in diameter. Sepals all biglandular, 2–3.5 mm long beyond the glands, 2.5–3.5 mm wide, obtuse or acute at the apex, abaxially densely appressed-tomentose, adaxially glabrous or distally tomentose, recurved at the apex in anthesis, accrescent (to ca twice as large) in fruit; glands 2–3.5 mm long, yellow. Petals yellow, turning red-orange in age, glabrous; lateral petals reflexed, with the claw 2.5–3.5 (–4) mm long, the limb 6–9 mm long, 7–11 mm wide; posterior petal with the claw 3–4.3 mm long, erect, eglandular, the limb 4–5.5 mm long, 5.5–7 mm wide, corrugated, reflexed. Filaments 2–3 mm long, abaxially glabrous, adaxially hirsute at the base; anthers 2.5–3.5 mm long, longer opposite sepals than petals, the locules glabrous, unwinged, often slightly free at the apex, the connective usually loosely sericeous outside locules and always sericeous between locules, often somewhat enlarged and flattened at the apex but not or hardly exceeding the locules (up to 0.4 mm). Ovary 1.8–2 mm high, densely woolly, all 3 locules fertile; styles 2.5–3.9 mm long, straight or bent away from the posterior petal. Fruit globose, to 3.7 cm in diameter, glabrate at maturity or persistently tomentose at the apex, yellow at maturity with thick juicy flesh, the nut 12 mm high and 18 mm wide, 3-lobed, deeply excavated at the base, leaving behind a rounded torus which fits into the excavation.

TYPE: BRAZIL. Mato Grosso: Mun. Rio Verde, Serra da Pimenteira, 25–35 km SW of town of Rio Verde, cerrado on sandy soil, 8 Feb 1975 fl/imm. fr, *Anderson 11274* (MBM, holotype; MICH, isotype).

PARATYPES: BRAZIL. Mato Grosso: Mun. Alto Araguaia, vic. of Riberão Claro, NW of Alto Araguaia, 800 m, cerrado, Feb fl, *Anderson 11404* (MICH); Cuiabá-Vilhena, Km 206, 56°28′ W, 14°11′ S, 550 m, campo cerrado, Mar fr, *Bamps 5498* (MICH); 12°54′ S, 51°52′ W, Xavantina-São Felix road, cerrado on red sandy soil, *R. R. de Santos et al. R.1244* (MO). Goiás: 12 km S of Caiapônia, 840 m, cerrado, Apr fl/fr, *Anderson 9518* (MICH, NY, UB); Mun. Rio Verde, open woodland, Jan fl/imm. fr, *Pedersen 12136* (MICH). Minas Gerais: 70 km S of Uberlândia, cerrado, Feb fl, *Anderson 12394* (MBM, MICH); Mun. Prata, cerrado, May fr (MICH); 9 km S of Frutal, cerrado, Mar fl, *Hatschbach 38223* (MICH); 4 km N of Patrocínio, 1000 m, cerrado, Jan fl, *Irwin et al. 25736* (MICH, NY); Mun. Frutal, sandy grassland with scattered trees, Jan fl, *Pedersen 12072* (MICH); Uberaba, *Regnell III 302* (MO).

Byrsonima affinis is closely related to *B. basiloba* Adr. Juss., a shrubby species which it resembles in herbarium specimens, which undoubtedly explains why it has not been named previously. The two species can be separated by the characters in the following couplet:

Tree (3–) 4–8 (–10) m tall, the trunk with thick, corky bark; lamina not only revolute at the margin but also undulate; anthers with the connective usually loosely sericeous outside locules and always sericeous between them; inflorescence pendent in fruit; fruit over 3 cm in diameter. *B. affinis.*

Shrub 0.3–1.5 (–2.5) m tall, much-branched from base, the stems not corky; lamina revolute at the margin but otherwise flat; anthers glabrous; inflorescence erect in fruit; fruit up to 2 cm in diameter. *B. basiloba.*

In addition to these differences, *B. basiloba* differs from *B. affinis* in the following tendencies: Its bracts are seldom revolute and mostly earlier deciduous; the anthers are generally shorter, probably seldom exceeding 2.5 mm in length; and the ovary is usually loosely sericeous instead of woolly, with the hairs straighter and more nearly parallel.

The distribution of *B. affinis* and *B. basiloba* is shown in Figure 5. For the most part the two species occur in different areas, but they seem to come very close together in the Triangulo Mineiro, south of Uberlândia. They should be studied in that area, to see whether they hybridize; perhaps they differ in ecological requirements that effectively separate them even there. The few collections of *B. basiloba* from the area of Vilhena, Rondônia, are disjunct from the rest of the species. They are somewhat atypical, especially in having smaller leaves and flowers, but they could not be assigned to any other species, certainly not to *B. affinis.* Further collection may reveal more populations of *B. basiloba* in cerrados across north-central Mato Grosso.

Byrsonima fonsecae W. R. Anderson, sp. nov. Fig. 6.

Arbor 5 m alta. Lamina foliorum majorum 10.5–15.5 cm longa, 5.5–7.5 cm lata, obovata vel paene elliptica, apice plerumque rotundata, subtus parce

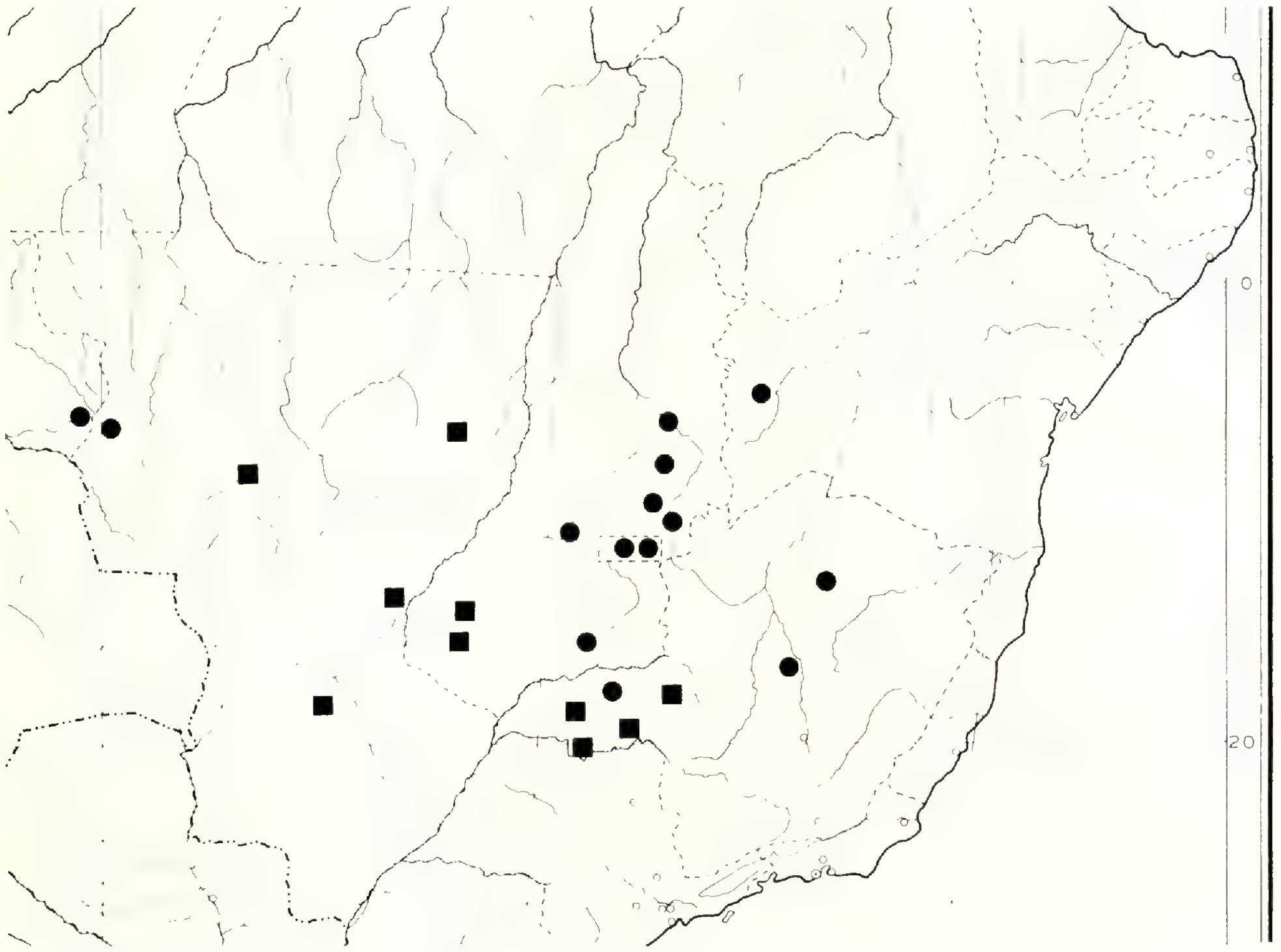

FIG. 5. Distribution of *Byrsonima affinis* (squares) and *B. basiloba* (circles). Goode Base Map 203, Copyright The University of Chicago.

appresso-tomentosa vel subsericea; petiolus 14–20 mm longus; stipulae 4–6 mm longae, omnino connatae vel apice distinctae. Inflorescentia bracteis 1.5–2.5 mm longis, 1.5–2 mm latis, persistentibus, pedunculis 1.5–6 (–10) mm longis, bracteolis bracteis similaribus vel minoribus. Pedicellus circinatus in alabastro, decurvatus in fructu. Sepala utrinque tomentosa, valde appressa per anthesin. Petala alba, demum rosea. Antherae glabrae, loculis cylindricis, 1.4–1.6 mm longis, connectivo 0.3–0.9 mm superatis. Fructus 12–13 mm diametro (siccus).

Tree 5 m tall, the stems thinly sericeous to glabrate. Lamina of the larger leaves 10.5–15.5 cm long, 5.5–7.5 cm wide, obovate or nearly elliptical, cuneate at the base, revolute at the margin, mostly rounded at the apex, sometimes emarginate, sometimes broadly obtuse, coriaceous and somewhat rugose above, soon glabrate above or loosely sericeous on the midrib and lateral veins, thinly appressed-tomentose or subsericeous below with some hairs straight and appressed and others twisted and spreading, eventually glabrescent, the lateral veins and reticulum visible above, prominent below; petiole 14–20 mm long, loosely sericeous to glabrate; stipules 4–6 mm long, completely connate or free just at the apex, abaxially sericeous to glabrate, adaxially glabrous. Inflorescence 4–12 cm long, loosely sericeous or tomentose to subvelutinous, the cincinni mostly 1-flowered, a few 2- or 3-flowered; bracts 1.5–2.5 mm wide, lanceolate or ovate, abaxially appressed-tomentose, adaxially glabrous, all or most persistent past maturity of the fruit; peduncle 1.5–6 (–10) mm long; bracteoles like the bracts or somewhat smaller, apical or 1 slightly subapical. Pedicel 7–8.5 mm long (somewhat longer in fruit), appressed-tomentose, circinate in bud, decurved and eventually twisted in fruit. Flower 13 mm in diameter. Sepals all biglandular, 1.5–2 mm long beyond the glands, 2–2.5 mm wide, obtuse or rounded, reddish-tomentose on both sides, strongly appressed in anthesis, somewhat accrescent in fruit (to ca 4 mm long and 5 mm wide); glands 2.5–3 mm long, pink. Petals glabrous, white, their claws becoming red or pink in age, the posterior petal with a yellow claw, the whole petal becoming red in age; lateral petals spreading, with the claw 3–3.5 mm long, the limb 4.5–5.5 mm long, 6–7 mm wide, concave, especially in the anterior pair; posterior petal erect, the claw 3 mm long and thicker, the limb 3.5–4.5 mm long, 4 mm wide, corrugated. Filaments 2–2.7 mm long, abaxially nearly glabrous, adaxially long-hirsute, especially on proximal ½; anthers 1.7–2.4 mm long, glabrous, the locules 1.4–1.5 mm long, cylindrical, separated on the connective, rounded and sometimes slightly detached at the apex, the connective yellow, extended 0.3–0.9 mm beyond the locules, the extension rounded or obtuse and somewhat recurved. Ovary ca 1.5 mm high, ovoid, glabrous, all 3 locules fertile; styles 3–3.5 mm long, white, all bent distally away from the posterior petal. Fruit 12–14 mm in diameter (dried), green, depressed-globose, short-beaked, glabrous, the nut prominently ribbed.

TYPE: BRAZIL. Minas Gerais: Serra do Cipó, ca 1225 m elev, in woods near stream, 18 Feb 1972 fl/fr, *Anderson et al. 36183* (UB, holotype; MICH, NY, isotypes).

Byrsonima fonsecae is named in honor of Sidney Geraldo da Fonsêca, plant collector, mechanic, and friend, whose diverse talents were critical to the success of many expeditions in central Brazil led by Howard Irwin, myself, and others. It seems to be most similar to *Byrsonima vernicosa* Niedenzu, a rare plant known only from near Petrópolis outside Rio de Janeiro, and *B. nervosa* DC., a species common in the Planalto of Brazil. All three have similar anthers, large fruits, pedunculate flowers, and large, petiolate, obovate, coriaceous leaves. However, *B. vernicosa* and *B. nervosa* have the leaves very densely and persistently tomentose below, whereas in *B. fonsecae* the lamina is only thinly hairy below at matu-

rity. Glaziou stated that *B. vernicosa* has yellow petals, but this requires confirmation, because all other species with anthers of this type have the petals white/pink.

Byrsonima souzae W. R. Anderson, sp. nov. Fig. 6.

Arbor 15 m alta. Lamina foliorum majorum 16–23.5 cm longa, 10.5–14 cm lata; petiolus 32–60 mm longus; stipulae 3–6 mm longae, omnino connatae. Inflorescentia floribus in cymulis 3-floris dispositis, bracteis 1–2 mm longis latisque, post maturitate fructus persistentibus, pedunculo 2–10 mm longo, bracteolis bracteis similibus vel minoribus, persistentibus. Petala rubra, glabra. Antherae glabrae, connectivo glanduloso loculos 1.2 mm superanti, conoideo. Ovarium sericeum; styli 2 mm longi, recti. Fructus 21–25 mm diametro, 10–13 mm altus; nux disciformis.

Tree 15 m tall, the trunk 13 cm in diameter; stems densely sericeous or appressed-tomentose with short, somewhat twisted hairs, eventually glabrescent. Lamina of the larger leaves 16–23.5 cm long, 10.5–14 cm wide, obovate or broadly elliptical, cuneate or rounded and often slightly decurrent at the base, rounded at the apex and often abruptly short-acuminate with the acumen up to 1 cm long, glabrate at maturity or sparsely appressed-tomentose on the midrib, especially below, the veins and reticulum prominent on both sides; petiole 32–60 mm long, sericeous like the stems to glabrate; stipules 3–6 mm long, smoothly and completely connate, rounded at the apex, abaxially appressed-tomentose to glabrate, adaxially glabrous. Inflorescence 15–18 cm long, appressed-tomentose like the stem, composed of short cymules of at least 3 flowers, possibly more; bracts 1–2 mm long and wide, broadly ovate, abaxially tomentose, adaxially glabrous; primary floriferous peduncle (from bract to joint) 2–10 mm long, longest at base of inflorescence and diminishing distally; peduncles of lateral branches of cymule apparently not developing; bracteoles like the bracts or smaller, the first bracteoles often borne below apex of peduncle; bracts and bracteoles persistent past maturity of fruit. Pedicel ca 5 mm long in flower, probably longer in fruit, tomentose, somewhat circinate in bud, perhaps straight in fruit. Flower ca 16 mm in diameter. Sepals all biglandular, ca 2 mm long beyond the glands, 2.5 mm wide, obtuse or rounded, abaxially appressed-tomentose, adaxially glabrous, strongly appressed in anthesis, wider but not or hardly longer in fruit; glands 3–4 mm long, white. Petals red, glabrous; lateral petals reflexed, with the claw 2–3 mm long, the limb 4–6 mm long, 5–6 mm wide; posterior petal erect or somewhat reflexed, the claw 2.5 mm long, the limb 3 mm long and wide. Filaments 2 mm long, abaxially glabrous, adaxially hirsute at the base; anthers 2.1–2.4 mm long, glabrous, the locules 0.9–1.2 mm long, unwinged, tapered distally to an acute apex, the connective enlarged and glandular, 1.7–1.8 mm long, extending ca 1.2 mm beyond the locules, tapered distally to a point, straight or somewhat recurved. Ovary 1.5 mm high, densely sericeous, all 3 locules fertile; styles 2 mm long, straight. Fruit 21–25 mm in diameter and 10–13 mm high, transversely depressed-obtrulloid, with the thin orange flesh following the contours of a disc-shaped nut, glabrate or sparsely sericeous distally.

BRAZIL. TYPE: Amazônas: Manaus, Km 45 da BR 17, t. firme, solo argiloso, mata virgem, 3 May 1961 fl, *Rodrigues & Coelho 2462* (INPA, holotype; NY, SP, isotypes). PARATYPE: Amazônas: Manaus, Estr. Torquato Tapajós, Km 105, lado direito, solo argiloso, Sep fr, *Rodrigues & Loureiro 7168* (INPA, NY).

This species is named in honor of my late friend, Raimundo Souza, a fine field botanist whose participation was a great asset to scores of expeditions led by

FIG. 6. *Byrsonima fonsecae* and *B. souzae*. a–h, *B. fonsecae*: a) flowering branch, × 0.5, with enlarged portion of abaxial side of lamina × 2; b) stipules, × 3.5; c) portion of inflorescence with pedunculate flower-bud, × 2.5; d) flower, × 2.5; e, f) stamens, × 10; g) gynoecium, with styles bent away from posterior petal, × 5; h) fruit, × 1.5. i–p, *B. souzae*: i) leaves and axis of inflorescence, × 0.5; j) stipules, × 1.5; k) reconstructed cymule, × 2.5; l) apex of peduncle to show bracteoles of cymule, × 7.5; m, n) stamens, × 10; o) gynoecium, × 7.5; p) fruit, with flesh and base in longitudinal section to expose the nut, × 0.75. Drawn by Karin Douthit, a–h from *Anderson et al. 36183*, i–o from *Rodrigues & Coelho 2462*, p from *Rodrigues & Loureiro 7168*.

both Brazilians and foreigners in all parts of Brazil. *B. souzae* is probably most closely related to *B. christianeae* Anderson, to which it is quite similar in most features, including the anthers and gynoecium. They differ in the inflorescence and fruit, both of which are unique in *B. souzae*. Its flowers are borne in stalked, dichasial cymules, with both bracteoles fertile, instead of one-sided, helicoid cymules (cincinni) as in other Malpighiaceae with compound inflorescences. I cannot tell from the material at hand whether more than three flowers develop in older cymules. *B. christianeae* has the flowers borne 1–3 in a cluster, actually a sessile cincinnus. The bizarre fruit of *B. souzae*, with a wide, depressed, disc-shaped nut, is quite different from the globose fruit of *B. christianeae* and all other species of *Byrsonima*.

Byrsonima spinensis W. R. Anderson, sp. nov. Fig. 2.

Arbor 4–6 m alta. Lamina foliorum majorum 4–8 (–9) cm longa, 1.8–3.2 (–3.6) cm lata, plerumque obovata, apice obtusa vel rotundata, glabrata vel paene glabrata; petiolus 6–9 (–10) mm longus; stipulae 1.6–2.3 mm longae, omnino connatae vel apice distinctae. Inflorescentia bracteis bracteolisque persistentibus, cincinnis 1–2-floris, pedunculo plerumque 1–5 mm longis. Pedicellus circinatus in alabastro, decurvatus in fructu. Sepala utrinque sparsissime sericea, valde appressa per anthesin. Petala alba, demum rosea. Antherae glabrae, loculis cylindricis, 1–1.6 mm longis, connectivo 0.7–1.1 mm superatis.

Tree 4–6 m tall, the stems initially sericeous (?), soon glabrate. Lamina of the larger leaves 4–8 (–9) cm long, 1.8–3.2 (–3.6) cm wide, obovate or sometimes elliptical, obtuse or rounded at the apex (sometimes abruptly short-acuminate), slightly revolute at the margin, tapered or cuneate at the base, soon glabrate or very sparsely sericeous below on the midrib, the lateral veins and reticulum visible but hardly prominulous; petiole 6–9 (–10) mm long, thinly sericeous to glabrate; stipules 1.6–2.3 mm long, completely connate or distinct just at the apex, smooth or sulcate in the middle, abaxially sericeous to glabrate, adaxially glabrous. Inflorescence 3–8 cm long, thinly sericeous to glabrate, the cincinni 1–2-flowered; bracts 1–2 mm long, ca 1 mm wide, triangular, glabrous or abaxially thinly sericeous, stiff; primary floriferous peduncle (from bract to joint) mostly 1–5 mm long, occasionally undeveloped; bracteoles like the bracts but smaller; bracts and bracteoles persistent at least past flowering. Pedicel (3.5–) 5–8 (–10) mm long, sericeous, moderately circinate in bud, decurved in old flowers and enlarging fruits. Flower 12–16 mm in diameter. Sepals all biglandular, 1.5–2.3 mm long beyond the glands, 2–2.5 mm wide, broadly obtuse or rounded, very sparsely sericeous on both sides and ciliate on the margin, strongly appressed in anthesis; glands white in bud, pink in anthesis, 1.6–2.5 mm long. Petals white, becoming pink in age, glabrous; lateral petals spreading to reflexed, the claw 2.5–3.5 mm long, the limb 4–5.5 mm long, 4.5–6 mm wide; posterior petal erect, the claw 2.7–3 mm long, the limb 3–3.5 mm long, 4–4.5 mm wide, corrugated. Filaments 2–2.5 mm long, sparsely hirsute abaxially at base, hirsute adaxially on proximal half; anthers 1.8–2.4 mm long, glabrous, the locules 1–1.6 mm long, cylindrical, rounded or minutely apiculate and sometimes slightly detached at the apex, the connective yellow, extended 0.7–1.1 mm beyond the locules, the extension conoid, bluntly pointed, nearly straight to recurved. Ovary 1–1.5 mm high, glabrous, all 3 locules fertile; styles 3.1–3.7 mm long, straight or bent away from the posterior petal. Fully enlarged fruit not seen.

TYPE: BRAZIL. Minas Gerais: Serra do Espinhaço, valley ca 5 km SSE of Pico de Itambé, 1140 m, by stream, 14 Feb 1972 fl, *Anderson et al. 35969* (UB, holotype; MICH, NY, isotypes).

PARATYPES: BRAZIL. Minas Gerais: Serra do Espinhaço, ca 8 km N of Gouveia on road to Diamantina, 1220 m, wet place at edge of gallery forest, Feb fl, *Anderson et al. 35339* (MICH, NY); same locality and date as type, *Anderson et al. 35970* (MICH, NY, UB).

This species is closely related to *Byrsonima myricifolia* Grisebach, which is also a much-branched tree with similar clusters of small, nearly glabrate leaves. They both have the petals all white, turning pink in age, the bracts and bracteoles persistent, and the floriferous peduncle usually well developed. *Byrsonima spinensis* differs from *B. myricifolia* in having the pedicel circinate in bud and in having many of the cincinni 2-flowered; in *B. myricifolia* the pedicels are straight, even in very young buds, and the cincinni seem never to bear a second flower. Also, the lamina is usually obtuse or rounded in *B. spinensis*, acuminate or acute in *B. myricifolia*.

The epithet *spinensis* refers to the elongated Serra do Espinhaço; *espinhaço* is a Portuguese word meaning backbone or spine.

Byrsonima bahiana W. R. Anderson, sp. nov. Fig. 3.

Arbor 8 m alta. Lamina foliorum majorum 8–10.5 cm longa, 4.3–5.6 cm lata, obovata, apice rotundata vel obtusa, coriacea, fere glabra; petiolus 14–16 mm longus; stipulae 1.5–2.5 mm longae, distinctae, rotundatae. Inflorescentia fere glabra, bracteis bracteolisque 1.2–1.5 mm longis, usque ad 1.9 mm latis, rotundatis, persistentibus. Pedicellus decurvatus in fructu. Sepala glandulas 2.5 mm superantia, apice rotundata, fere glabra, in fructu carnosa et accrescentia, minimum 10 mm longa et 9 mm lata, basi auriculata. Petala alba et rosea. Antherae 2–2.5 mm longae, glabrae, loculis ut videtur nec complanatis nec alatis, connectivo vix superatis (0.1 mm). Ovarium glabrum, tantum 2 loculis fertilibus. Fructus immaturus ca 15 mm diametro.

Tree to 8 m tall, the trunk 20 cm in diameter; stems initially very thinly sericeous, soon quite glabrate except short-hirsute in axils of stipules. Lamina of larger leaves 8–10.5 cm long, 4.3–5.6 cm wide, obovate to almost elliptical, rounded or obtuse at the apex, revolute at the margin, cuneate at the base, coriaceous, tinged with red above, especially on margin and midrib, glabrous or bearing a few straight appressed hairs on the midrib below, not glaucous below, not or slightly glaucous above, the principal lateral veins ca 10, prominulous below; petiole 14–16 mm long, glabrous or bearing a few straight appressed hairs; stipules 1.5–2.5 mm long, distinct, broadly rounded, inserted so that one stands partially inside the other, glabrous. Inflorescence 10.5–11 cm long, sericeous at the very base, distally very sparsely sericeous to glabrate, the flowers borne 1 per bract; bracts 1.2–1.5 mm long, 1.6–1.9 mm wide, broadly rounded, glabrous or bearing a few hairs; peduncle none; bracteoles about as long as the bracts but narrower, usually not as wide as long; bracts and bracteoles persistent past maturity of the fruit. Pedicel in fruit 10–13 mm long, bearing scattered appressed hairs, decurved. Sepals all biglandular, 2.5 mm long beyond the glands, 3 mm wide, rounded, glabrous except for tiny hairs on the margin, revolute in anthesis, appressed and greatly enlarged in fruit; glands 2.5–3 mm long. Petals "strongly reflexed with reddish claw and small concave white limb, often tinged with pink," persistent in immature fruit. Filaments 2–3 mm long, abaxially glabrous, adaxially hirsute at base; anthers 2–2.5 mm long, glabrous, the locules apparently not flattened or winged, exceeded only slightly (0.1 mm) by the connective. Ovary 1.5 mm high, glabrous, with only 2 locules developed and fertile. Immature fruit ca 15 mm in diameter, with thick flesh around a small nut ca 5–6 mm in diameter, glabrous; accrescent sepals fleshy, appressed, at least 10 mm long and 9 mm wide, somewhat auriculate at the base.

TYPE: BRAZIL. Bahia: 5 km SE of Maraú, 39°00′ W, 14°08′ S, low restinga on sand, elev. 0–50 m, 2 Feb 1977 fr, *Harley 18475* (CEPEC, holotype; MICH, isotype).

This species is readily placed in Niedenzu's series *Platylepis* on the basis of its white and pink petals, distinct stipules, and small, subequal, persistent bracts and bracteoles. It is most similar to *Byrsonima laevis* Niedenzu and *B. amoena* Cuatrecasas. The most dramatic characteristic distinguishing *B. bahiana* is its fleshy sepals that are large in flower and enlarge greatly in fruit. In contrast to the dimensions given above for this species, the sepals of *B. laevis* and *B. amoena* are only 1.5 mm long or less in flower and enlarge to no more than 4 mm long in fruit. In *B. bahiana* the calyx glands, filaments, and anthers are longer than in *B. laevis* and *B. amoena*; also, the anther locules in *B. bahiana* do not appear to be flattened and winged as in the other two species, and the ovary has only two locules fertile instead of three. Additional differences may become apparent when good flowering material of *B. bahiana* is available for study. The type bears immature fruits and my only flowers were old, degraded, and incomplete.

Byrsonima laevis and *B. amoena* are species of northwestern Amazonia, in the drainage area of the Rio Negro in Brazil, Venezuela, and Colombia. *B. bahiana* is known only from the type, which was collected 2500 km from Manaus, where *B. amoena* grows, and even farther from the nearest populations of *B. laevis*. The Amazonian affinities of many species of coastal Bahia have been abundantly documented, but this is still an impressive disjunction. Also, it is worth noting that this is a species of white-sand restinga, not wet forest as is true of many species or species-pairs disjunct between Bahia and Amazonia. *Byrsonima laevis* and *B. amoena* are also species of open, white-sand vegetation, the Rio Negro analogue of the restingas of Bahia. This suggests that when the Amazonian flora extended down the coast into Bahia, it probably comprised not only forests, but white-sand "campinas," just as it does today.

Byrsonima alvimii W. R. Anderson, sp. nov. Fig. 7.

Arbor usque ad 20 m alta. Lamina foliorum majorum 12–18 cm longa, 5.5–9.3 cm lata, omnino vel fere glabra; petiolus 18–25 mm longus; stipulae 5–7 mm longae, omnino connatae, glabrae. Inflorescentia bracteis 4–7 mm longis, 2–3.3 mm latis, reflexis, demum deciduis (?), cincinnis 1–3-floris, pedunculo (0–) 1–4.5 mm longo, bracteolis bracteis similibus, 2.5–4 mm longis, plerumque non reflexis. Pedicellus circinatus in alabastro. Sepala utrinque velutina vel sericea. Petala rosea. Antherae loculis sericeis vel hirsutis praecipue apice, cylindricis, 1.5–2.1 mm longis, apice rotundatis, connectivo (0.4–) 0.7–1.1 mm superatis. Ovarium glabrum; styli 4.5–5 mm longi.

Tree to 20 m tall, the trunk 35 cm in diameter; stems nearly glabrous except hirsute in axils of stipules. Lamina of the larger leaves 12–18 cm long, 5.5–9.3 cm wide, elliptical, acute or obtuse and apparently abruptly falcate at the apex, revolute at the margin, cuneate at the base, coriaceous, glabrous or with a few appressed hairs on the midrib below, the principal lateral veins 8–10, moderately prominent below; petiole 18–25 mm long, glabrous or very sparsely sericeous; stipules 5–7 mm long, smoothly and completely connate, the pair broadly triangular, wider than the petiole, glabrous. Inflorescence 13–16 cm long, sericeous proximally to velutinous distally; cincinni 1–3-flowered, the second and third flowers more likely to develop in proximal cincinni; bracts 4–7 mm long, 2–3.3 mm wide, flat, lanceolate, mostly strongly reflexed, loosely and sparsely sericeous to glabrate; primary floriferous peduncle (0–) 1–4.5 mm long, longest in proximal cincinni, velutinous; bracteoles like the bracts but smaller (2.5–4 mm long, 1.2–2.5 mm wide), mostly not reflexed; bracts and bracteoles

FIG. 7. *Byrsonima alvimii* and *B. morii*. a–e, *B. alvimii*: a) flowering branch, × 0.5; b) stipules, × 2.5; c) cincinnus, with 1 posterior-lateral petal removed from flower, × 2.5; d) stamens, × 7.5; e) gynoecium, with tips of styles bent away from posterior petal, × 5. f–j, *B. morii*: f) flowering branch, × 0.5, with reticulum of upper surface of lamina × 1.5; g) stipules, × 2.5; h) flower, × 2.5; i) stamens, × 7.5; j) gynoecium, with anterior style to left, × 5. Drawn by Karin Douthit from the types.

apparently deciduous late in anthesis or afterwards. Pedicel 9–11 long, velutinous, circinate in bud. Flower 18 mm in diameter. Sepals all biglandular, 1.5–2 mm long beyond the glands, 2.5 mm wide, obtuse, densely velutinous or sericeous on both sides, erect or revolute at the apex in anthesis; glands 2.5–3.5 mm long. Petals pink, glabrous; lateral petals reflexed, the claw 3.5–4 mm long, the limb 6–8 mm long, 7–9 mm wide; posterior petal erect, the claw 4 mm long, the limb 5 mm long and wide, corrugated. Filaments 3–3.5 mm long, abaxially glabrous or sparsely hirsute at base, adaxially densely red-hirsute on proximal ½ and sometimes sparsely hirsute distally; anthers 1.9–3.2 mm long, longest opposite 3 anterior sepals and shortest opposite 3 posterior petals, the locules 1.5–2.1 mm long, cylindrical, sericeous or hirsute, especially at the apex, rounded and sometimes detached at the apex, the connective yellow, massive, extended 0.7–1.1 mm beyond the locules (only 0.4 mm in anther opposite posterior petal), the extension truncated or bluntly pointed, straight or slightly recurved. Ovary 1.8 mm high, glabrous, all 3 locules fertile; styles 4.5–5 mm long, bent in the distal ½–⅓. Fruit not seen.

TYPE: BRAZIL. Bahia: Una, Faz. São Rafael, mata, 10 Nov 1969 fl, *T. S. dos Santos 479* (CEPEC, holotype; MICH, isotype).

PARATYPE: BRAZIL. Bahia: Ubaitaba-Maraú, Dec fl, *Vinha 53* (CEPEC, MICH).

Another collection that may well represent this species is *Pinheiro 1691* (or 1601?) (MICH). It was a tree 15 m tall, collected in forest on the road from Santa Luzia to Canavieiras, Bahia. The material is in very young bud, so that color of the petals was not known, but the anthers do seem to be hairy and the connective exceeds the locules. It resembles *B. alvimii* in the size and shape of the leaves, bracts, and bracteoles, but all parts of the plant are much hairier and the stipules are smaller.

Byrsonima alvimii is named in honor of Dr. Paulo de T. Alvim, who as Scientific-Technical Director at CEPLAC has played an important role in encouraging collection and study of the flora of Bahia.

This species falls into Niedenzu's series *Psilonemis*, due to its pink petals and hairy anthers with an extended connective. Within that group, it seems to have no close relatives. It is distinguished by its stature, large coriaceous petiolate leaves, 1–3-flowered cincinni with the peduncle often developed, very large bracts and bracteoles, and sepals densely hairy on both sides. It seems to be most similar to *B. schomburgkiana*, but I am not convinced that they are really very closely related.

According to the label on the type, the common name of this species is "mucambo roxo."

Byrsonima surinamensis W. R. Anderson, sp. nov. Fig. 4.

Arbor 6–17 m alta, ramis sericeis. Lamina foliorum majorum 5–8.5 (–10) cm longa, 2.4–3.7 cm lata, anguste obovata, apice plerumque rotundata vel emarginata, mucronata; petiolus 2–4 (–5) mm longus, laxe sericeus vel demum glabrescens. Inflorescentia bracteis bracteolisque caducis, pedunculo nullo, floribus singulis. Pedicellus 4–5.5 mm longus (–10 mm in fructu), rectus vel paulo circinatus in alabastro, decurvatus vel tortus in fructu. Petala rosea. Antherae 1.4–2.8 mm longae, loculis 0.8–1.0 mm longis, cylindricis, distaliter laxe sericeis, apice rotundatis vel acutis, connectivo loculos 0.6–1.8 mm superanti. Ovarium glabrum; styli 2.5 mm longi. Fructus sepalis accrescentibus, usque 6–8 mm longis, distaliter 3–4 mm latis, lingulatis, proximaliter auriculatis, membranaceis.

Tree 6–17 m tall, the trunk 15–30 cm in diameter; stems densely sericeous, glabrescent only belatedly; internodes mostly very short, the leaves borne in dense apical clusters. Lamina of the larger leaves 5–8.5 (–10) cm long, 2.4–3.7 cm wide, obovate or narrowly obovate, gradually narrowed to cuneate at the base, broady obtuse or (usually) rounded or emarginate and mucronate at the apex, glaucous below, glabrate at maturity except loosely sericeous on the midrib, especially below, and on the apical mucro, with scattered appressed hairs persistent elsewhere on the lamina, the lateral veins prominulous below or on both sides; petiole 2–4 (–5) mm long, loosely sericeous or eventually glabrescent; stipules 2–3.5 mm long, smoothly connate but the pair usually emarginate at the apex, abaxially sericeous, adaxially glabrous. Inflorescence 6–12 cm long, velutinous-tomentose; flowers borne 1 per bract; bracts 2.5–3.5 mm long, ca 1 mm wide, narrowly lingulate, spreading and ± straight, abaxially loosely sericeous, adaxially glabrous or sparsely sericeous in the center; peduncle none; bracteoles like the bracts but shorter; bracts and bracteoles deciduous before anthesis. Pedicel 4–5.5 mm long (–10 mm in fruit), appressed-tomentose, straight or slightly circinate in bud, decurved or sigmoid-twisted in fruit. Sepals all biglandular, 2 mm long beyond the glands, ca 2 mm wide, ovate-lingulate, strongly revolute in anthesis, abaxially appressed-tomentose, especially in the center, and ciliate on the margin, adaxially loosely sericeous proximally, accrescent (especially elongated) in fruit; glands 1.8–2.4 mm long, reddish. Petals pink, glabrous, the outermost covering all others in bud; lateral petals reflexed, with the claw 2.5–3 mm long, the limb 5–6.5 mm long, 5.7–7.3 mm wide, concave, especially in the anterior pair; posterior petal erect, the claw 3 mm long and thicker, the limb 4 mm long, 4.5 mm wide, corrugated. Filaments 1.5–2 mm long, longer opposite petals than sepals, abaxially glabrous, adaxially hirsute on the proximal ½; anthers 1.4–2.8 mm long (in the same flower), loosely sericeous on the locules, especially distally, the locules 0.8–1.0 mm long, rounded or acute and slightly detached at the apex, cylindrical, the connective extended 0.6–1.8 mm beyond the locules, the extension cylindrical, blunt, straight or the longer ones recurved, longest on anterior stamens and shortest on posterior. Ovary 1.5 mm high, ovoid, glabrous, all 3 locules fertile; styles 2.5 mm long, straight. Fruit ca 9–10 mm in diameter, glabrous; accrescent sepals 6–8 mm long, distally 3–4 mm wide, lingulate, basally somewhat auriculate, membranous.

TYPE: SURINAME. Lely Mts., 175 km SSE of Paramaribo, east slope of plateau no. 1, 500–700 m, 10 Oct 1976 fr, *Mori & Bolten 8437* (MICH, holotype; NY and 7 undistributed duplicates, isotypes).

PARATYPES: SURINAME. Nassau Mts., savanna forest near km 11.6, 16 Mar sterile, *Lanjouw & Lindeman 2737* (IAN); Lely Mts., SW plateaus covered by ferrobauxite between 550 and 710 m alt., along base line on plateau 5 in low savanna-like forest on ferrite, 30 Sep fl, *Lindeman et al. 597* (MO, NY).

Byrsonima surinamensis is similar to *B. schomburgkiana* Bentham, a species known from southern Guyana and adjacent Brazil and Venezuela. *B. schomburgkiana* differs in the following characteristics: More twisted hairs of stems and leaves, producing a vesture that I would call tomentose; larger and especially wider leaves that are more gradually tapered distally, with a longer petiole; persistent bracts and bracteoles; longer pedicels; anthers with longer locules (1.3–1.9 mm) and the connective extended only 0.5–1.1 mm beyond the locules; longer styles. For a full description, see p. 98 of my Guayana Highland paper (1981).

Byrsonima aubletii Kostermans, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 25: 10. 1936, *nom. nov.* for *B. altissima* (Aublet) DC.

Malpighia altissima Aublet, Hist. Pl. Guiane Franç. 1: 455. 1775, not *M. altissima* Jacquin, 1764. Type: *Aublet,* French Guiana, "in sylvis Sinemariensibus" (BM!).

Byrsonima altissima (Aublet) DC. Prodr. 1: 579. 1824.

Byrsonima discolor Pilger, Repert. Spec. Nov. Regni Veg. 42: 179. 1937. Type: *Ducke,* Brazil, Pará, ilhas altas do Macujubinsinho (RB 20950!).

Tall tree, 18–30 m tall. Lamina of the larger leaves 10–15 cm long, 5.5–8 cm wide, elliptical or obovate, obtuse or rounded and often abruptly short-acuminate at the apex, sericeous to glabrate at maturity above, densely and persistently rufous-sericeous below, the reticulum prominent above; petiole 20–33 mm long, sericeous; stipules 3–4 mm long, completely connate, abaxially sericeous, adaxially glabrous. Inflorescence with the flowers borne 1 per bract; bracts and bracteoles alike, very small, ca 0.5–1 mm long and wide, broadly triangular or rounded, persistent past maturity of the fruit; peduncle 0–0.5 mm long. Pedicel 8–10 mm long (–16 mm in fruit), straight in bud, nodding in fruit. Sepals all biglandular or all eglandular, abaxially densely sericeous, adaxially sparsely sericeous, especially proximally. Petals white or pink (probably white turning pink in age), abaxially densely sericeous. Anthers densely sericeous, with some hairs on the locules and many more on the connective between the locules and outside beside them; locules extended at the apex into long, tapered, distally sterile horns about equalling the connective; connective enlarged at the apex into a swollen, globular or elongated mass, larger in some anthers than others in the same flower. Ovary densely sericeous; all 3 locules fertile. Immature fruit ovoid, with an apical beak, thinly sericeous.

In 1935, Sandwith pointed out that the correct name for *Byrsonima altissima sensu* Niedenzu (1928) is *B. aerugo* Sagot. Not only is the epithet *altissima* illegitimate; its type was not the species for which Niedenzu used the name. However, Sandwith did not know which species was actually represented by Aublet's type. Kostermans did not understand the taxonomy of *Byrsomina* even as well as Sandwith, but he went ahead anyway and published the substitute name *B. aubletii.* When I was able to study Aublet's type in 1981, I discovered that the species is the one described in 1937 as *B. discolor* Pilger. The only difference between Aublet's collection and the others I have seen, which have all come from Pará or Maranhão, is that the latter have eglandular sepals while Aublet's specimen has all the sepals biglandular. The occurrence of eglandular forms is very common in *Byrsonima* species and does not merit taxonomic recognition.

Byrsonima aubletii is quite distinctive. Its anthers are those of Niedenzu's Section *Acrotheca* Subsection *Uroceras.* In that group this is the only species with the leaves densely and persistently sericeous below and the petals sericeous. In fact, this is the only species in the genus with densely hairy petals. In a few others (e.g. *B. maguirei*) the petals bear a few hairs, but in most the petals are glabrous. The brief description given above is intended to facilitate recognition of this rare and interesting plant, which is not described in Niedenzu's 1928 monograph.

HETEROPTERYS

These species, like those of *Byrsonima,* are presented here in approximately the order of their closest relatives in Niedenzu's monograph (1928).

Heteropterys actinoctenia W. R. Anderson, sp. nov. Fig. 8.

Liana lignosa. Lamina foliorum majorum 7–10.5 cm longa, 3.5–4.2 cm lata, falcata, elliptica, apice acuminata, glabrata, subtus inter costam et marginem aliquot glandulis parvis munita; petiolus 6–9 mm longus, eglandulosus. Inflorescentia paniculata, 3–4 cm longa, ex 3–5 umbellis vel corymbis 3–8-floris constans; pedunculus 4–6 mm longus, apice vel saepius infra apicem bibracteolatus. Calycis glandulae 3.2–4 mm longae, obovatae, decurrentes. Nux samarae utrinque 4–8 alulis parallelis ex areola ventrali radiantibus munita.

Woody vine; stems sericeous to glabrate, with many punctiform lenticels. Lamina of the larger leaves 7–10.5 cm long, 3.5–4.2 cm wide, falcate, elliptical, acuminate at the apex, thin and ± flat at the margin, rounded at the base, initially sericeous? quite glabrate at maturity, bearing on each side below a row of small (0.5 mm in diameter) crateriform glands approximately midway between midrib and margin, shiny above, the lateral veins and reticulum visible below, barely so above; petiole 6–9 mm long, glabrate or bearing scattered appressed hairs at maturity, eglandular; stipules not found. Inflorescence axillary and terminal, 3–4 cm long, a raceme of 3–5 short-stalked or subsessile umbels or corymbs of 3–8 flowers each, tomentose-sericeous; floriferous bracts 1–1.5 mm long, triangular, concave, appressed, eglandular, persistent; peduncle 4–6 mm long; bracteoles like the bracts or smaller, one or both usually borne up to 1 mm below apex of peduncle. Pedicel 8 mm long (in fruit), tomentose-sericeous. Sepals (in fruit) triangular, flat (not revolute), 1.5–2 mm long, ca 2 mm wide, hardly exceeding the glands, abaxially tomentose, adaxially glabrous, the anterior eglandular, the lateral 4 bearing 8 large glands 3.2–4 mm long, obovate, compressed, somewhat decurrent onto pedicel. Petals and stamens unknown. Style stigmatic on the inner angle of the apex, briefly extended dorsally and rounded or obtuse. Samaras 30–40 mm long, brown-sericeous, especially proximally and toward abaxial edge of wing; dorsal wing 25–32 mm long, 12–16 mm wide, often with a rounded projection on adaxial edge near nut, the abaxial margin straight or slightly curved upward; nut ca 6 mm long and high, bearing on each side a series of 4–8 short parallel winglets oriented at right angles to margin of ventral areole, irregular in size and shape, the largest 2.5 mm wide, often alternating with much smaller outgrowths; ventral aerole ovate, 3–4 mm high, 2–2.5 mm wide; pyramidal torus ca 2 mm high.

TYPE: PERU. Loreto: Prov. Maynas, upland forest remnant and adjacent scrub on white sand just past Quistococha, ca 200 m, 27 May 1978 fr, *A. Gentry 22302 & N. Jaramillo* (MICH, holotype).

Heteropterys actinoctenia resembles *H. cristata* Bentham and *H. floridana* Cuatr. in its leaves and inflorescence, so I assume it will prove to have pink carinate or winged petals when it is found with flowers. It differs from both of them, and from all other species in the genus, in its samara, which bears on the nut a series of parallel winglets oriented at right angles to the margin of the ventral aerole. The epithet *actinoctenia* refers to this "radiating comb"; it is the name Niedenzu gave to the section of *Banisteria (Banisteriopsis)* in which this kind of samara occurs. In other species of *Heteropterys* the nut of the samara is smooth-sided or bears on each side a single transverse winglet oriented parallel to the margin of the ventral areole. The samara of *H. cristata* and *H. floridana* is of the latter type. *Heteropterys actinoctenia* is also distinguished by its somewhat decurrent calyx glands and its relatively short peduncles and pedicels, which produce an inflorescence denser than that of its close relatives.

FIG. 8. *Heteropterys actinoctenia* and *H. marleneae*. a–e, *H. actinoctenia*: a) fruiting branch, × 0.5; b) infructescence, × 1; c) old flower after loss of samaras, with pedicel and part of peduncle, × 2.5; d) tip of style, × 25; e) base of samara, × 2. f–i, *H. marleneae*: f) fruiting branch, × 0.5; g) pseudoraceme with 2 old flowers, × 2.5; h) tip of style, × 25; i) immature samara, × 10. Drawn by Karin Douthit from the types.

Heteropterys Series **Rhodopetalis** Niedenzu Subseries **Stenostigma** Niedenzu

In his treatment of *Heteropterys* for Das Pflanzenreich, Niedenzu divided the pink-flowered species into two principal subseries, *Bradystigma* and *Stenostigma,* plus a third subseries for the Antillean species, *H. purpurea.* The most important difference between the first two lay in the stigmas, which are dorsiventrally compressed in two or all three styles in *Bradystigma,* laterally compressed in *Stenostigma.* Study of the species assigned to *Stenostigma* by Niedenzu has led me to remove the following species, for the reasons given:

H. rubiginosa Adr. Juss.: The type proves to have the styles of *Bradystigma.*
H. trichanthera Adr. Juss.: The petals are yellow.
H. machaerophora Nied.: Two of the three styles are dorsiventrally compressed as in *Bradystigma.*
H. martiana Adr. Juss.: The petals are yellow; this species is probably related to *H. syringifolia* Grisebach.
H. dusenii Nied.: The petals are yellow.

This leaves only *Heteropterys pteropetala* Adr. Juss. in *Stenostigma. H. pteropetala* is a widespread, polymorphic species that merits careful study, which will probably result in its division into several entities. I am not prepared to address that problem at this time, but there are two additional species of *Stenostigma* in eastern Brazil that seem to be distinct from *H. pteropetala.* They are decribed below.

Heteropterys caducibracteata W. R. Anderson, sp. nov. Fig. 9.

Frutex usque ad 2 mm altus vel liana lignosa. Lamina foliorum majorum 3–4.8 cm longa, 1.6–2.5 cm lata, utrinque pertinaciter tomentosa, subtus 0, 1, vel 2 glandulas prope basim ferens; petiolus 3–4 mm longus, eglandulosus. Bracteae 1.8–2.5 mm longae, 0.4–0.5 mm latae, anguste triangulares vel ellipticae, eglandulosae, deciduae; bracteolae bracteis similares sed persistentes. Petala rosea et alba; petala lateralia dorsaliter alata, ala alba, pilosa, 0.6–1 mm lata; petalum posticum dorsaliter carinatum. Filamenta inaequalia, illa sepalis opposita plerumque longiora, illa petalis postico-lateralibus opposita crassissima, 3 postica inter stylos posticos inflexa; antherae 0.9–1.1 mm longae.

Shrub to 2 m tall or woody vine climbing to 4 m; stems to 3 cm in diameter, tomentose-sericeous, belatedly glabrescent. Lamina of the larger leaves 3–4.8 cm long, 1.6–2.5 cm wide, elliptical or ovate, acute or obtuse at the apex, flat at the margin, cuneate at the base, persistently tomentose or subvelutinous above with stalked, mostly T-shaped sinuous hairs, persistently densely tomentose below, bearing 0, 1, or 2 slightly peltate glands below near base between midrib and margin, the lateral veins prominent below, obscure above; petiole 3–4 mm long, appressed-tomentose, eglandular; stipules 0.2 mm long, triangular, borne on petiole above its base. Inflorescence paniculate, densely tomentose, the flowers borne in corymbs or dense racemes of 10–20 (or more?); bracts 1.8–2.5 mm long, 0.4–0.5 mm wide, narrowly triangular or elliptical, thin, abaxially densely tomentose, adaxially glabrous or sparsely tomentose, eglandular, deciduous late in anthesis; peduncle 5–7.5 mm long, densely tomentose; bracteoles like the bracts or slightly shorter, persistent (at least through anthesis; older stages not seen), borne at or slightly below apex of peduncle. Pedicel 2.5–4.5 mm long, densely tomentose. Flowers ca 12 mm in diameter. Sepals 1.5–2 mm long, 1–1.3 mm wide, triangular, obtuse at the apex, appressed in anthesis, abaxially densely and uniformly tomentose, adaxially glabrous, the anterior eglandular or bearing 1 or 2 glands, the lateral 4 all biglandular, the glands 1.2–1.6 mm long, pink. Petals pink with white wings, pilose especially on the wings; lateral petals

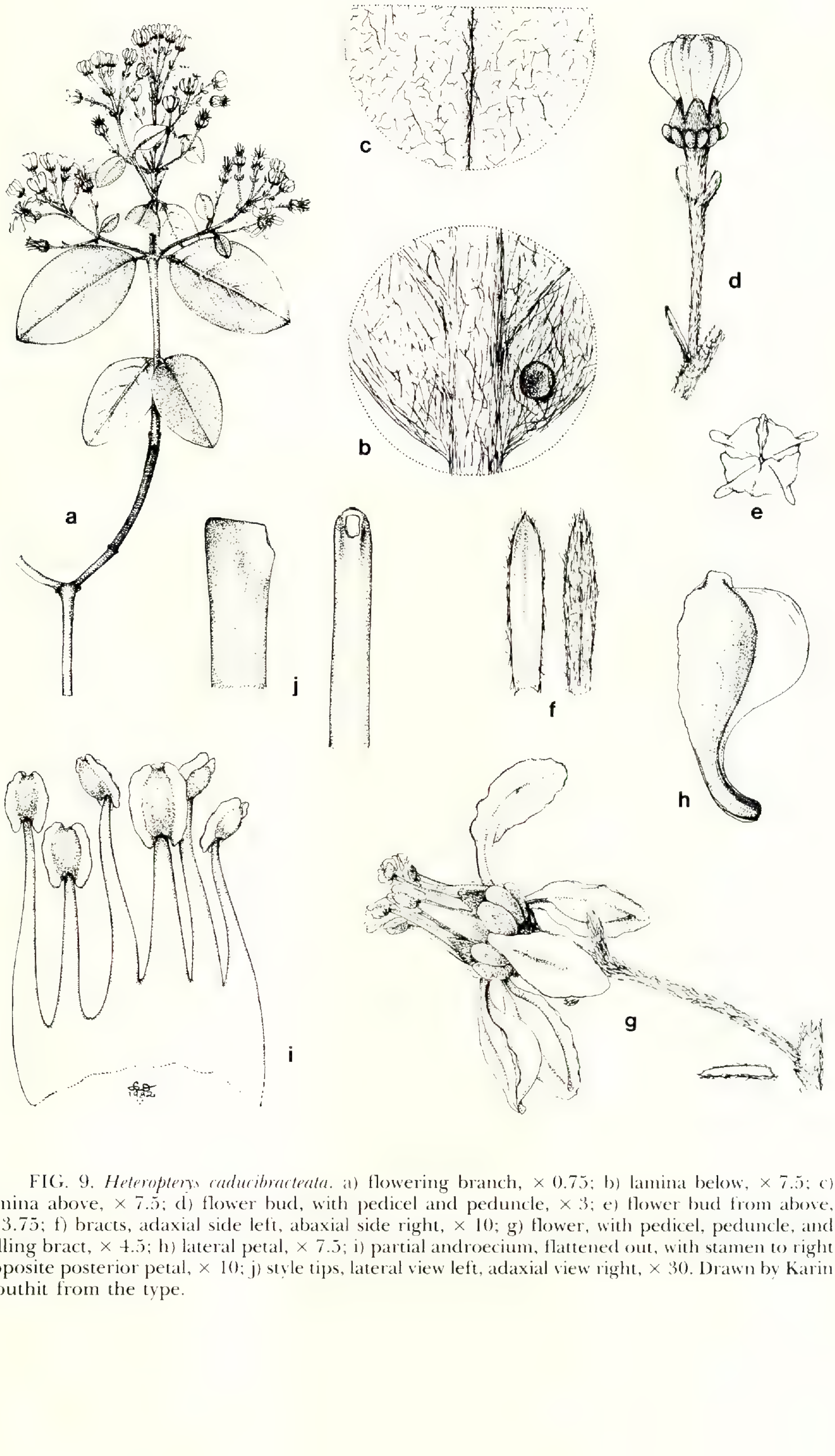

FIG. 9. *Heteropterys caducibracteata*. a) flowering branch, × 0.75; b) lamina below, × 7.5; c) lamina above, × 7.5; d) flower bud, with pedicel and peduncle, × 3; e) flower bud from above, × 3.75; f) bracts, adaxial side left, abaxial side right, × 10; g) flower, with pedicel, peduncle, and falling bract, × 4.5; h) lateral petal, × 7.5; i) partial androecium, flattened out, with stamen to right opposite posterior petal, × 10; j) style tips, lateral view left, adaxial view right, × 30. Drawn by Karin Douthit from the type.

spreading to reflexed, the winged claw 1.5–2 mm long, the limb 3.5–4.5 mm long, 2–2.3 mm wide, elliptical, entire or slightly erose, eglandular, bearing a prominent decurrent dorsal wing 0.6–1 mm wide; posterior petal erect with the limb reflexed, the claw 2.8–3.5 mm long, 1 mm wide, the limb 3.3–4 mm long, 2.3–2.7 mm wide, oblong, erose, eglandular, dorsally carinate with the keel 0.2 mm wide, decurrent. Filaments red in age, 2.2–3.5 mm long, connate in the basal 0.8–1 mm, glabrous, unequal, generally longer opposite sepals than petals, thickest opposite posterior-lateral petals, the posterior 3 inflexed; anthers glabrous, 0.9–1.1 mm long, subequal, largest opposite posterior-lateral petals. Ovary 1.5 mm high, densely sericeous; styles 1.7–2.2 mm long, equal or the anterior slightly shorter, ± straight, somewhat divergent, flattened laterally, truncate dorsally at the apex, the stigma internal and elliptical. Fruit unknown.

TYPE: BRAZIL. Bahia: Caatinga between Breijão da Caatinga and Delfino (41°0–20′ W, 10°25′ S), sandy soil, 600 m, 9 km W of Breijão, 7 Mar 1976 fl, *Anderson 11742* (MBM, holotype; MICH, isotype).

Heteropterys caducibracteata is named for its deciduous bracts, which fall late in anthesis, in contrast to the persistent bracts of the other species of *Stenostigma*. The bracts and bracteoles are also unusual in their narrowly elliptical shape and thin texture. The leaves in this species are smaller than in *H. perplexa* and *H. pteropetala sens. lat.*, in which the larger laminas are at least 6 cm wide, and usually quite a bit larger.

Heteropterys perplexa W. R. Anderson, sp. nov. Fig. 10.

Liana lignosa. Lamina foliorum majorum 6.5–13.5 cm longa, 3.8–8 cm lata, ovata vel elliptica, subtus pertinaciter subvelutina et 2 magnis glandulis prope basim munita; petiolus 5–6 mm longus, eglandulosus. Bracteae bracteolaeque persistentes; pedunculus 5–9 mm longus. Pedicellus 3–5.5 mm longus. Sepala abaxialiter sericea. Petala limbo albo et roseo, ungue rubro; petala lateralia dorsaliter alata, ala 1.2–2.5 mm lata; petalum posticum dorsaliter carinatum, carina 0.1–0.3 mm lata. Filamenta rubra, valde inaequalia, illa petalis antico-lateralibus opposita brevissima, illa petalis postico-lateralibus opposita crassissima, 3 postica inter stylos posticos inflexa.

Woody vine climbing to 10 m; stems densely appressed-tomentose or subsericeous, eventually glabrescent. Lamina of the larger leaves 6.5–13.5 cm long, 3.8–8 cm wide, ovate or elliptical, acute or slighty acuminate at the apex, flat at the margin, broadly cuneate to rounded at the base, appressed-tomentose to glabrate above, persistently subvelutinous below with T-shaped hairs with the trabecula much longer than the stalk and straight or sinuous, bearing 2 large, often swollen or slightly peltate glands abaxially above the base, on the midrib or on a lateral vein between midrib and margin, the lateral veins and coarse reticulum prominent below, impressed above; petiole 5–6 mm long, appressed-tomentose to glabrescent, eglandular; stipules 0.2 mm long, borne on the petiole just above its base. Inflorescence paniculate with widely spreading branches, densely tomentose, containing reduced leaves with 2 large protuberant and sometimes short-stalked glands, the flowers borne in umbels or tight corymbs of 4–15; bracts 1.3–1.8 mm long, 0.6–1 mm wide, triangular or ovate, abaxially densely and uniformly tomentose, adaxially glabrous, appressed, eglandular, persistent (at last while peduncle persists); peduncle 5–9 mm long, densely tomentose; bracteoles 1–1.5 mm long, 0.8–1 mm wide, triangular or ovate, abaxially tomentose in center and glabrate and membranous toward margin, adaxially glabrous, spreading, usually bearing 2 small marginal glands or glandular spots near the base, persistent, borne at or just below apex of peduncle. Pedicel 3–

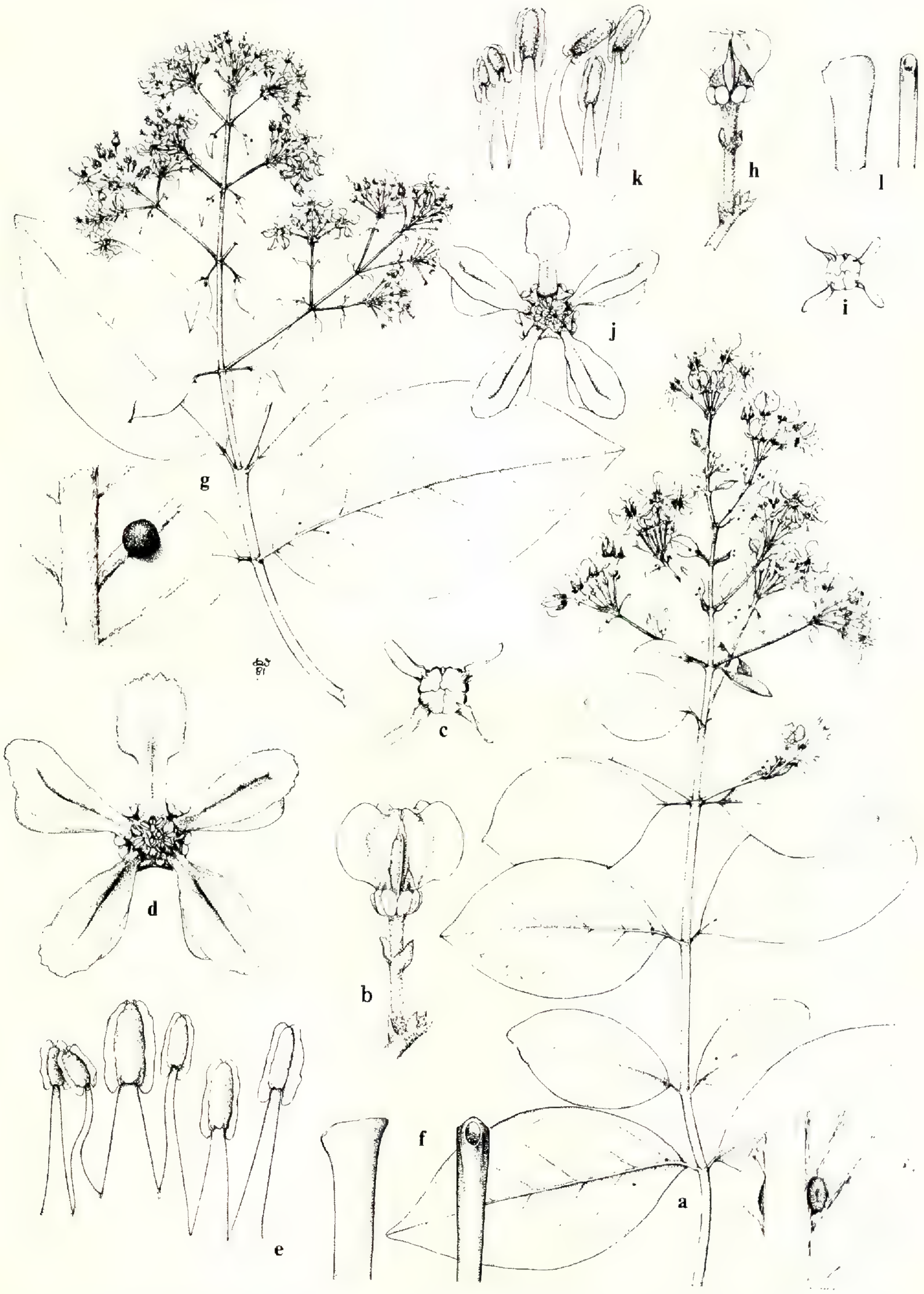

FIG. 10. *Heteropterys perplexa*. a, g) flowering branches, × 0.5, with circles × 7.5; b, h) flower buds with pedicel and peduncle, × 2; c, i) flower buds from above, × 2.5; d, j) flowers from above, × 3; e,k) partial androecia, flattened out, with stamen to left opposite posterior petal, × 7.5; f, l) style tips, lateral view left, adaxial view right, × 20. Drawn by Karin Douthit, a–f from *Anderson 11749*, g–l from *Irwin et al. 23203*.

5.5 mm long, densely tomentose. Flowers 10–16 mm in diameter. Sepals 1.5–2 mm long, 1–2 mm wide, triangular, acute or obtuse at the apex, appressed in anthesis, abaxially uniformly sericeous or glabrous at the margin, adaxially glabrous, the anterior eglandular, the lateral 4 bearing 8 glands 1.3–2 mm long. Petals white on the margins, pink in the center, and red in the claw, glabrous or sparsely pilose on edge of wing; lateral petals spreading, the winged claw 1.1–2 mm long, the limb 3–5.5 mm long, 2–3.3 mm wide, elliptical, entire, eglandular, bearing a prominent dorsal wing 1.2–2.5 mm wide; posterior petal erect with the limb somewhat reflexed, the claw 2–3 mm long, 1–1.4 mm wide, the limb 2.3–3.5 mm long and wide, irregularly rectangular, revolute, slightly erose, eglandular, dorsally carinate with the keel 0.1–0.3 mm wide, decurrent. Filaments red, 1.5–3.5 mm long, connate in the basal 0.5–1 mm, glabrous, strongly unequal, shortest opposite anterior-lateral petals, thickest opposite posterior-lateral petals, the posterior 3 bent inward between the 2 posterior styles; anthers glabrous, unequal, 0.9–1.8 mm long, shortest opposite the 4 lateral sepals and the posterior petal. Ovary 1–1.5 mm high, densely sericeous; styles 2–3 mm long, glabrous, straight and erect or divergent or leaning toward posterior petal, flattened laterally, rounded or truncate or apiculate dorsally at the apex, the stigma internal and elliptical. Fruit unknown.

TYPE: BRAZIL. Bahia: Caatinga 10–20 km W of Delfino on road from Lagoinha to Campo Largo, 41°20′ W, 10°27′ S, 650–750 m, 8 Mar 1976 fl, *Anderson 11749* (MBM, holotype; K, MICH, NY, RB, US, isotypes).

PARATYPES: BRAZIL. Bahia: 8 km NW of Lagoinha, 5.5 km SW of Delfino, on road to Minas do Mimoso, caatinga/cerrado, frequently burned and cut over, ca 850 m, ca 41°17′ W, 10°24′ S, Mar fl, *Harley 16775* (MICH). Minas Gerais: Serra do Espinhaço, wooded valley slopes, ca 5 km NE of Francisco Sá, road to Salinas, 950 m, Feb fl, *Irwin et al. 23203* (MICH, NY, UB).

I originally intended to describe this as two species, one based on *Anderson 11749*, the other on *Irwin et al. 23203*. They have flowers that are dramatically different in size, with petal-wings 2–2.5 mm wide vs. 1.2–1.5 mm wide, respectively, and longest filaments 3–3.5 mm long vs. 2.5 mm. Figure 10 was drawn to illustrate those and other differences. Then I realized that *Harley 16775* is generally similar to my *11749* and came from the same area, but has flowers that are somewhat intermediate in size, especially in the petal-wings, which are 1.5–1.7 mm wide. Since the three collections are similar in most vegetative features, it seems best to treat them as one species, at least for the present. Perhaps when more collections are available it will become possible to achieve a finer resolution of this perplexing situation.

The only character that reliably separates this species from *H. pteropetala* Adr. Juss. *sensu lato* is habit. *Heteropterys perplexa* is a woody vine, while *H. pteropetala* is an erect subshrub, shrub, or small tree. The common form of *H. pteropetala* differs further in having larger suborbicular leaves with denser hairs below. As noted above, *H. pteropetala* requires thorough study.

Heteropterys krapovickasii W. R. Anderson, sp. nov. Fig. 11.

Liana lignosa. Lamina foliorum majorum 7.5–10.5 cm longa, 3.5–5.1 cm lata, eglandulosa, subtus pertinaciter metallo-sericea; petiolus 7–13 mm longus, 2 glandulas magnas inter medium et apicem ferens. Inflorescentia paniculata, foliis minoribus petiolo vel basi laminae biglandulosis et saepe margine laminae aliquot glandulis minoribus munitis; flores in umbellis vel corymbis (2–) 4–8-floris portati, saepe 1–2 paribus proximalibus adjectis; bracteolae plerumque prope medium pedunculi portatae. Petala flava, ungue 1.3–2.4 mm longo, limbo 3–4 mm longo, 2.3–3 lato. Filamenta 1.7–2.5 mm longa, recta; antherae 1–

1.1 mm longae, glabrae. Styli recti. Samara 23–30 mm longa; ala dorsalis 13–15 mm lata, flabelliformis.

Woody vine, the stems puberulent to glabrate. Lamina of the larger leaves 7.5–10.5 cm long, 3.5–5.1 cm wide, elliptical or slightly obovate, obtuse, rounded, or emarginate and often apiculate at the apex, flat or slightly recurved at the margin, cuneate or obtuse at the base, eglandular (but see inflorescence leaves), initially sericeous above but soon glabrate or persistently sericeous on the midrib, very densely and persistently metallic-sericeous below, the hairs both brown and white, sometimes abraded from oldest leaves, the lateral veins prominent below, the reticulum visible above; petiole 7–13 mm long, sericeous to glabrate, bearing 2 large glands between middle and apex; stipules not found. Inflorescence

FIG. 11. *Heteropterys krapovickasii*. a) fruiting branch, × 0.55, circle × ca 2.8; b) base of leaf, abaxial side, × 1.65; c) portion of inflorescence in fruit, × 2.2; d) samara, × 1.1; e) flower, × 3.85; f) petals, posterior petal left, lateral petal right, × 5.5; g) portion of androecium, opened out, abaxial view, stamen to left opposite posterior petal, × 8.25; h) tip of style, side view, × 22. Drawn by Karin Douthit, a–d from *Pires & Santos 16372*, e–h from *Krapovickas & Schinini 36259*.

paniculate, subvelutinous or appressed-tomentose, containing abruptly reduced leaves with large glands on petiole or base of lamina and often several smaller glands distally on margin of lamina; flowers borne ultimately in umbels or corymbs of (2–) 4–8 flowers, often with 1 or 2 additional pairs of flowers borne more proximally; bracts 0.9–1.2 mm long, 0.5–0.8 mm wide, ovate, appressed, abaxially sericeous, adaxially glabrous, eglandular, persistent; peduncle (1.5–) 2.5–4 mm long; bracteoles like the bracts but slightly shorter (0.7–1 mm long), borne mostly near middle of peduncle, sometimes somewhat above or below. Pedicel 3–5.5 mm long, appressed-tomentose. Flowers 10–11 mm in diameter. Sepals 2–2.5 mm long, 1.5–1.7 mm wide, triangular or ovate, obtuse or rounded at the apex, appressed in anthesis, abaxially sericeous, adaxially glabrous, all eglandular or the lateral 4 bearing 7–8 glands 1.1–1.4 mm long, elliptical, separated on the sepals. Petals yellow, glabrous, eglandular, nearly entire (minutely denticulate or erose); lateral petals horizontal, ± spatulate, with the claw 1.3–1.7 mm long, the limb 3–4 mm long, 2.3–3 mm wide, ovate or broadly elliptical, somewhat concave; posterior petal apparently erect, hardly different in size and shape from the lateral 4, the claw 2–2.4 mm long, the limb 3 mm long, 2.3–2.5 mm wide, truncate at the base. Filaments 1.7–2.5 mm long, mostly shorter and stouter opposite petals than sepals, straight, glabrous, basally connate; anthers 1–1.1 mm long, alike, glabrous. Ovary 1 mm high, densely sericeous; styles 2.2 mm long, straight and ± erect, equalling or slightly exceeding the anthers, truncate and acute or slightly apiculate dorsally at the apex. Samaras 23–30 mm long, sparsely sericeous; dorsal wing 23–30 mm long, 13–15 mm wide, extending over the adaxial edge of the nut, much flared distally to produce a flabellate shape, the abaxial margin nearly straight; nut 6 mm long, 5 mm high, with prominent parallel longitudinal wrinkles (dried) but no lateral crests or wings; ventral areole circular, 1.5–2 mm in diameter.

TYPE: BOLIVIA. Santa Cruz: Prov. Sandoval, San Matías (58°26′ W, 16°21′ S), 5 km SW del Aeropuerto, 170 m, 19 Apr 1980 fl, *Krapovickas & Schinini 36259* (MICH, holotype; CTES, NY, isotypes).

PARATYPE: BRAZIL. Mato Grosso: 57°50′ W, 14°48′ S, capoeira de mata seca, Aug fr, *Pires & Santos 16372* (MICH, MG).

This species is named in honor of my friend, Antonio Krapovickas, a fine botanist who specializes in the systematics of the Malvaceae.

Heteropterys krapovickasii is closely related to *H. hassleriana* Nied., from which it differs chiefly in having the hairs on the abaxial side of the lamina very dense, straight, sessile, appressed, and persistent, producing a metallic-sericeous vesture. In *H. hassleriana* the hairs are sparser and less appressed and the leaf is usually soon glabrate. Also, in *H. hassleriana* the samara wing is not or hardly flared distally, so that the two edges of the wing are nearly parallel. Both of these species are probably closely related to the larger-flowered *H. tomentosa,* although Niedenzu placed *H. tomentosa* and *H. hassleriana* in different subsections.

Heteropterys sincorensis W. R. Anderson, sp. nov. Fig. 12.

Frutex vel arbor parva usque ad 3 (–4) m alta. Lamina foliorum majorum (5–) 6–10 cm longa, 4.5–6.5 cm lata, coriacea, late ovata vel elliptica vel suborbicularis, apice rotundata et interdum apiculata vel emarginata, basi rotundata vel cordata, mox glabrata, basi margine 2 glandulas magnas impressas et interdum distaliter aliquot glandulas minores marginales ferens; petiolus 2–4 mm longus, eglandulosus. Pedunculus (1.5–) 4–7 mm longus, apice bibracteolatus. Sepala appressa, plerumque omnia biglandulifera, glandulis sericeis. Petala flava, abaxialiter rubra in centro, denticulata; petalum posticum limbo basi glanduloso. Androecium glabrum. Styli apice truncati vel interdum apiculati.

FIG. 12. *Heteropterys sincorensis*. a) flowering branch, × 0.5, with leaf below enlarged in circle to left and upper surface in circle to right, both × ca 2.5; b) base of leaf, abaxial view, × 3; c) umbel, × 2.5; d) flower, × 3.5; e) petals, abaxial view, anterior-lateral (left) and posterior (right), × 3.5; f) anthers, abaxial view (left) and adaxial view (right), × 10; g) style-tip, × 20; h) samara borne on receptable, × 1. Drawn by Karin Douthit, a–g from *Harley 18821*, h from *Mori et al. 12635*.

Samarae ala dorsalis 23–27 mm longa, 11–14 mm lata, nux sine cristis lateralibus.

Shrub or small tree up to 3 (–4) m tall; stems loosely sericeous, soon glabrescent. Lamina of the larger leaves (5–) 6–10 cm long, 4.5–6.5 cm wide, broadly ovate or elliptical to suborbicular, rounded and sometimes apiculate or emarginate at the apex, slightly revolute at the margin, rounded or cordate at the base, coriaceous, at first sparsely sericeous but soon glabrate, bearing 2 large impressed marginal glands at base of blade or halfway onto petiole and often additional smaller glands distally in marginal sinuses, the lateral veins and coarse reticulum prominent below, the fine reticulum prominent above; petiole 2–4 mm long, thick, loosely sericeous to glabrate, eglandular except for the often decurrent glands at base of lamina; stipules often present on petioles of small inflorescence-leaves as minute (0.1–0.2 mm long) protuberances borne on petiole above base, apparently absent from larger leaves. Inflorescence a much-branched, many-flowered panicle containing abruptly reduced leaves, the ultimate branches sometimes racemose but usually corymbose or umbellate comprising 4–10 or more flowers, loosely sericeous; bracts and bracteoles 1–2 mm long, 0.5–1 mm wide, elliptical or obovate, rounded at the apex, appressed, persistent, the bracteoles borne at apex of peduncle, usually bearing 2 tiny marginal glands at the base; peduncle (1.5–) 4–7 mm long. Pedicel 5–10 mm long, loosely sericeous. Flowers 11–13 mm in diameter, "very sickly scented" (*Harley 15981*). Sepals 1.6–2 mm long, 1.2–1.5 mm wide, ovate or triangular, acute or obtuse at the apex, appressed in anthesis, abaxially sericeous, adaxially glabrous, all biglandular or (in 1 collection) the anterior eglandular, the glands 1.5–2.5 mm long, obovate, densely sericeous, attached below free portion of sepal. Petals yellow with red abaxial streak, turning orange-red in age, glabrous; lateral petals spreading to eventually strongly reflexed, with the claw 1–1.8 mm long, winged, the limb 3.5–4.5 mm long, 2–3 wide, oblong or obovate, denticulate and eglandular at the margin, thickened and slightly carinate in the middle; posterior petal with the claw 1.5–2.3 mm long, thick and winged, erect, the limb 3–3.5 mm long, 2.3–3 mm wide, reflexed, similar to lateral petals but with glandular zones or discrete glands at the base. Filaments 1.5–2.5 mm long, longer opposite sepals than petals, erect and straight, connate in the proximal 0.7–1.3 mm, glabrous; anthers 1–1.4 mm long, glabrous, subequal. Ovary ca 1.5 mm high, densely sericeous; styles 1.5–2 mm long, glabrous, alike, erect to eventually divergent with the anterior bending back toward the anterior sepal and the posterior 2 bending toward the posterior petal, equalling or slightly exceeding the anthers, truncate at the apex, sometimes minutely apiculate dorsally. Samaras 30–35 mm long, borne quite erect when single, suberect when 2 develop, reddish purple (dried), sparsely and loosely sericeous; dorsal wing 23–27 mm long, 11–14 mm wide, the abaxial margin nearly straight; nut 6–7 mm long, 4–5 mm high, with prominent veins but no lateral crests or wings; ventral areole ovate or circular, ca 3 mm in diameter; torus ca 2.5 mm high.

TYPE: BRAZIL. Bahia: Serra do Sincorá, by Rio Cumbuca ca 3 km S of Mucugé, near site of small dam on road to Cascavel, approx. 41°21′ W, 13°01′ S, 850 m, 4 Feb 1974 fl, *Harley 15981* (CEPEC, holotype; MICH, isotype).

PARATYPES: BRAZIL. Bahia, Serra do Sincorá: 5 km S of Andaraí on road to Mucugé, by bridge of Rio Paraguaçú, 41°19′ W, 12°50′ S, ca 400 m, Feb fl, *Harley 18587* (MICH); 2–3 km SW of Mucugé on road to Cascavel, open scrub on white sand, 41°24′ W, 13°01′ S, ca 950 m, Feb fl, *Harley 18821* (MICH); 6.5 km SW of Mucugé on Cascavel road, sandstone rock and sandy soils, 41°25′ W, 13°01′ S, ca 1000 m, Mar fl, *Harley 21019* (MICH); Mpio de Mucujê, na estrada para Jussiape, 41°24′ W, 13°00′ S, 1000 m, campo rupestre, Jul fr, *Mori et al. 12635* (MICH, US).

This distinctive species is notable for its arborescent habit, glabrate coriaceous leaves with marginal glands and short petioles, umbels or corymbs of pedunculate flowers, hairy calyx glands, oblong yellow petals with a red abaxial streak, and the flag petal with glands at the base of the limb. It is probably most similar to *Heteropterys bahiensis* Nied., known only from the type, which I have not seen. The photograph of the specimen at G (F neg. 24258) shows it to have relatively long, narrowly elliptical leaves, cuneate at the base, with slender, well developed petioles. When *H. bahiensis* is collected with good flowers and fruits, further differences from *H. sincorensis* will surely be found. *Heteropterys sincorensis* is known only from the Serra do Sincorá, for which it is named; the place of origin of Blanchet's type of *H. bahiensis* is not known. Other species in this complex are *H. megaptera* Adr. Juss., from Rio de Janeiro, and *H. lasseri* Anderson, from Venezuela.

Heteropterys conformis W. R. Anderson, sp. nov. Fig. 13.

Liana lignosa, ramis mox glabratis. Lamina foliorum majorum 5.5–9.5 (–12.5) cm longa, 3–4.5 (–5.7) cm lata, margine tenuis, primo sericea permox omnino glabrata, reticulo utrinque ± prominenti; petiolus 7–15 mm longus, basi biglandulosus. Inflorescentiae axillares et terminales, 1.5–4 cm longae, floribus congestis. Pedicellus 4–7 mm longus, 0.3–0.4 mm diametro, sessilis. Sepala appressa per anthesin, eglandulosa. Petala flava, valde reflexa, limbo 2–2.5 mm longo, 1.8–2.3 mm lato. Styli angulo interno stigmatici.

Woody vine; stems initially sericeous, soon glabrate. Lamina of the larger leaves 5.5–9.5 (–12.5) cm long, 3–4.5 (–5.7) cm wide, elliptical, rounded, obtuse, or acute at the apex, sometimes emarginate or abruptly short-acuminate, thin and slightly revolute at the margin, cuneate to rounded at the base, initially sericeous but very soon quite glabrate, eglandular or (*Glaziou 13608*) bearing several small glands on or just within the margin, the lateral veins and reticulum prominent on both sides; petiole 7–15 mm long, sericeous to soon glabrate, biglandular at or just above the base, the glands circular, slightly raised, 0.7–1.3 mm in diameter; stipules not found. Inflorescence a series of dense axillary and terminal clusters, borne among current leaves, each unit 1.5–4 cm long, sericeous, a raceme of sessile and stalked umbels of 2–6 flowers with some flowers borne singly on the axis; bracts and bracteoles 0.5–1 mm long, narrowly ovate or triangular, eglandular, persistent; floriferous peduncle none. Pedicel 4–7 mm long, 0.3–0.4 mm in diameter, sericeous. Flowers 6–8 mm in diameter. Sepals 2–2.5 mm long, 0.9–1.5 mm wide, ovate or elliptical, rounded at the apex, appressed in anthesis, abaxially loosely sericeous, adaxially glabrous, all eglandular. Petals yellow, glabrous; lateral petals soon strongly reflexed, the claw 1.2–1.8 mm long, the limb 2–2.5 mm long, 1.8–2.3 mm wide, ovate, concave, denticulate, eglandular; posterior petal hardly different from the lateral 4, the limb or limb and claw strongly reflexed, the claw 1.5–2.5 mm long, the limb 2–2.5 mm long, 2 mm wide, ovate, bearing tiny glandular-thickened zones at the base or tiny sessile glands around the margin. Filaments 1.5–2 mm long, connate in the proximal 0.5–0.7 mm, strongly unequal, stoutest and straightest opposite the 2 posterior-lateral petals, the posterior 3 bent inward, glabrous; anthers 0.8–1.2 mm long, largest opposite posterior-lateral petals, glabrous, the connective dark red to black. Ovary 1–1.3 mm high, tomentose; styles 1.7–2.2 mm long, equalling or slightly exceeding the stamens, glabrous, nearly straight to somewhat arcuate, laterally flattened, truncate at the apex or dorsally acute, stigmatic on the inner angle. Fruit unknown.

TYPE: BRAZIL. Bahia: Itajú do Colônia a 25 km da estrada Itajú–Pau Brasil, solo pedregoso em capim, 23 Jan 1969 fl, *T. S. Santos 346* (CEPEC, holotype; MICH, isotype).

FIG. 13. *Heteropterys conformis* and *H. sanctorum*. a–f, *H. conformis*: a) flowering branch, × 0.5, circles × 2.5; b) petiole, × 2.5; c) portion of inflorescence, × 3.5; d) flower, × 5; e) androecium, stretched out, abaxial view, with stamen to left opposite anterior sepal, × 10; f) gynoecium, × 7.5. g–m, *H. sanctorum*: g) leaf, abaxial view, × 0.5, circle × 2.5; h) inflorescence on old stem, × 0.5; i) portion of inflorescence, × 2.5; j) flower, × 5; k) portion of androecium, × 5; l) gynoecium, anterior style to left, × 7.5; m) style-tip, × 25. Drawn by Karin Douthit from the types.

PARATYPES: BRAZIL. Minas Gerais: Biribiry, près de Diamantina, 1882, *Glaziou 12491* (C, G, P); Rio Manso, *Glaziou 13608* p.p. (P).

I doubt that either of the paratypes actually came from Minas Gerais. For some reason, Glaziou falsified the label data for many of his collections, ascribing to Rio de Janeiro or Minas Gerais plants that very probably came from Bahia or farther north. *Glaziou 18925a*, the type of *Byrsonima glazioviana* Nied., is *B. crispa* Adr. Juss. and surely came from Bahia or north, not Minas Gerais. Another example is *Glaziou 9680*, which is *Peixotoa jussieuana* Adr. Juss.; Glaziou said it came from Rio de Janeiro, whereas it probably came from Maranhão, Piauí, or Ceará (C. Anderson, pers. comm.).

This species, and the next two, belong to the series *Holopetalum*, which I would define as comprising species with appressed sepals, yellow petals, sessile pedicels, and the lamina not persistently metallic-sericeous below. *Heteropterys conformis* is quite similar to *H. ternstroemiifolia*, and the epithet chosen denotes that similarity. The two species can be distinguished by the characteristics summarized in the following couplet:

Inflorescence axillary and terminal, 1.5–4 cm long, the flowers densely crowded; calyx eglandular; lamina initially sericeous but very soon quite glabrate, the margin thin, the reticulum ± prominent below; limb of petals 2–2.3 mm long, 1.8–2.3 mm wide; stigmas strongly internal. *H. conformis.*

Inflorescence terminal, 2–14 cm long, open; calyx bearing 8 glands on the 4 lateral sepals; lamina initially densely tomentose, usually glabrate at maturity, the margin thickened and cordlike, the reticulum invisible below; limb of petals 3–4.5 mm long, 2.5–3 mm wide; stigmas terminal or subterminal. *H. ternstroemiifolia.*

Heteropterys ternstroemiifolia Adr. Juss., Ann. Sci. Nat. 2° Sér. Bot. 13: 274. 1840. Type: *Martius 116*, "in sylvis caeduis ad latera montium prope Sebastianopolim et Mandiocca," Rio de Janeiro, Brazil (M! holotype; M! probable isotype, P! isotype).

Banisteria fischeriana Regel & Koernicke, Ind. sem. horti Petrop. 48. 1858. Type: *Riedel 173*, Corcovado, Rio de Janeiro, Brazil, Jan 1832 fl (LE! lectotype; GH! LE! U! W! isolectotypes or isosyntypes).

Banisteria ternstroemiifolia (Adr. Juss.) Nied., Verz. Vorles. Ak. Braunsberg 1912–1913: 14. 1912.

Woody vine, the stems sericeous to glabrate, longitudinally fissured and bearing punctiform lenticels in age, occasionally rooting at the nodes. Lamina of the larger leaves 6.5–13 cm long, 2–6 cm wide, elliptical or obovate, cuneate or occasionally rounded at the base, thickened and cordlike at the margin and sometimes corrugated, acute to rounded and often apiculate and retuse at the apex, initially densely rusty-tomentose on both sides, soon glabrescent, usually nearly or quite glabrate at maturity and often shining above, eglandular, the lateral veins and reticulum obscure or prominulous above, obscure below; petiole 8–15 (–20) mm long, appressed-tomentose to glabrate, biglandular at the base, the glands circular, 0.5–1.5 mm in diameter; stipules subulate, ca 0.5 mm long, borne at base of petiole just below glands. Inflorescence 2–14 cm long, open, loosely sericeous to glabrate, terminal, simple or occasionally basally ternate, a raceme of sessile or stalked umbels or corymbs of 2–6 flowers each, the umbels often subtended by biglandular bracts; floriferous bracts 0.7–1 (–1.5) mm long, triangular, eglandular, persistent; peduncle none; bracteoles like the bracts but smaller, usually ca 0.5 mm long. Pedicel 4–10 mm long, loosely sericeous, tumid at the apex, thickening in fruit, especially toward the apex. Sepals 2–3.5 mm long, 1.5–2 mm wide, ovate, acute or rounded at the

apex, appressed in anthesis, abaxially loosely sericeous, adaxially glabrous or sericeous at the margin, the anterior eglandular, the lateral 4 bearing 8 elliptical glands, the glands 1.4–2.5 mm long, free and sometimes revolute at the apex, not compressed. Petals yellow, glabrous, all 5 very strongly reflexed [flipped completely back] in anthesis, the claw 1.5–1.7 mm long, the limb 3–4.5 mm long, 2.5–3 mm wide, obovate, convex in center, revolute at margin, the margin eglandular, erose or denticulate; posterior petal hardly different from the lateral 4, the limb slightly longer. Filaments 2–3 mm long, alike, straight, connate for about ½ their length, glabrous on both sides; anthers 1–1.6 mm long, alike, glabrous, erect to reflexed. Ovary 1.5 mm high, reddish-tomentose, 3-lobed, all 3 locules fertile; styles 1.5–1.8 mm long, equalling or slightly exceeding the stamens, glabrous, straight, diverging from each other, truncate at the apex, stigmatic on the apex or on the oblique inner angle. Samara 38–45 mm long, sparsely tomentose on the nut at maturity, otherwise glabrate; dorsal wing 25–31 mm long, 15–18 mm wide, extending over the adaxial side of the nut, the abaxial margin bent abruptly upward beyond the nut; nut 12–15 mm long, 7–10 mm high, the sides bulging and without winglets or crests, the veins prominent, the ventral aerole ovate to circular, 5 mm high, 4 mm wide.

BRAZIL. Rio de Janeiro: 1832 fl, *Ackermann* (BR); 1851 fl, *Andersson* (S); 1847 fl, *Forssell 111* (S); Copacabana, 29 Oct 1867, *Glaziou 2116* (BR, C, P); Corcovado loco umbroso, 15 Sep 1874 fr, *Mosén 2441* (S); Copacabana, Aug 1862 fr, *Nadeaud* (P).

This species is endemic to the immediate area of Rio de Janeiro. I have described it in full here because Niedenzu's description, under *Banisteria,* is inadequate. I have seen no collection made more recently than 1874, which makes me fear that the species is extinct. However, perhaps it is hiding in some "loco umbroso" at the foot of Corcovado.

Heteropterys sanctorum W. R. Anderson, sp. nov. Fig. 13.

Liana lignosa. Lamina foliorum majorum 18–25 cm longa, 8–11 cm lata, subtus pertinaciter sparsim sericea, margine aliquot glandulis parvis munita; petiolus 15–22 mm longus, basi biglandulosus. Inflorescentia in ramis vetustioribus portata, 4–8 cm longa. Pedicellus 6.5–9 mm longus, 0.5–0.8 mm diametro, sessilis. Sepala appressa per anthesin, 4 lateralia 6–8 glandulas ferentia. Petala flava, valde reflexa, inter se similaria.

Woody vine, the stems sericeous to glabrate. Lamina of the larger leaves 18–25 cm long, 9–11 cm wide, ovate, elliptical, or obovate, mostly acuminate at the apex, slightly revolute at the magin, cuneate, obtuse, or rounded at the base, initially sericeous but soon glabrescent, with persistent scattered hairs below at maturity, bearing a series of small sessile marginal or very slightly (to 1.5 mm) submarginal glands, often in sinuses, the lateral veins visible above, lateral veins and reticulum prominent or at least visible below; petiole 15–22 mm long, sericeous to glabrate, biglandular at the base, the glands 2 mm in diameter; stipules not found. Inflorescence borne on old, leafless stems, axillary to fallen leaves, 4–8 cm long, sericeous, an open unbranched raceme of stalked or sessile umbels of 2–4 flowers, with some flowers borne singly on the axis, the small bracts (2 mm long) bearing 2 large glands; floriferous bracts and bracteoles ca 0.5 mm long, ovate, sericeous, eglandular, persistent; floriferous peduncle none. Pedicel 6.5–9 mm long, 0.5–0.8 mm in diameter, sericeous. Flower ca 12 mm in diameter. Sepals 1.5 mm long beyond the glands, 1–1.5 mm wide, triangular, appressed in anthesis, abaxially sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 bearing 6–8 glands (4 on the posterior-lateral 2, 1–2 each on the anterior-lateral 2), the glands 1.4–1.7 mm long, circular or elliptical.

Petals yellow, glabrous, all completely reflexed, the lateral 4 with the claw 1.5–1.8 mm long, the limb 3.5–4 mm long, 2.7 mm wide, obovate, erose or denticulate, eglandular, the posterior like the others or the limb slightly wider. Filaments 2.2–2.5 mm long, subequal, connate in the proximal 1 mm, glabrous, those opposite the sepals pressed inward, those opposite the petals leaning outward; anthers 1–1.5 mm long, slightly longer opposite sepals than petals, glabrous, reflexed. Ovary 1.5 mm high, loosely sericeous; styles 2–2.5 mm long, glabrous, strongly divergent, truncate at the apex, stigmatic on the upper-internal angle. Fruit unknown.

TYPE: BRAZIL. Bahia: São José, estrada a Una, Pedra branca, mata, 6 May 1971 fl, *T. S. dos Santos 1603* (CEPEC, holotype; MICH, isotype).

PARATYPE: BRAZIL. Bahia: Uruçuca/Ubaitaba, Apr imm fl, *Santos 761* (CEPEC).

This species is named in honor of Talmon Soares dos Santos, who collected both the type and the paratype. Mr. Santos has made many fine collections in a previously neglected region and thereby contributed much to Brazilian botany.

Heteropterys sanctorum is most similar to *H. transiens* Nied., which seems to be endemic to the area of Rio de Janeiro. They are compared in the characters known for both in the following couplet:

Inflorescence 4–8 cm long, without long lateral branches, borne on old, leafless stems; larger laminas 8–11 cm wide, with all glands nearly or quite marginal; petiole 15–22 mm long. *H. sanctorum.*

Inflorescence 15–30 cm long, compound, axillary and terminal on currently leafy stems; larger laminas 11–15 cm wide, bearing a row of glands 5–15 mm inside the margin; petiole 30–50 mm long. *H. transiens.*

Heteropterys marleneae W. R. Anderson, sp. nov. Fig. 8.

Liana lignosa. Lamina foliorum majorum 15–17 cm longa, 7.3–8.5 cm lata; petiolus 13–16 mm longus, 3–4 glandulis immersis munitus. Inflorescentia axillaris, paniculata, 10–20 cm longa, floribus in pseudoracemis 2–6 cm longis, 6–26-floris, tomentoso-velutinis portatis; bracteae 1–1.5 mm longae lataeque, 2 glandulis prominentibus munitae, persistentes; pedunculus nullus vel interdum usque ad 0.5 mm longus; bracteolae bracteis similares sed minores et eglandulosae. Pedicellus 5 mm longus. Sepala apice revoluta.

Woody vine. Lamina of the larger leaves 15–17 cm long, 7.3–8.5 cm wide, elliptical or obovate, obtuse or abruptly short-acuminate at the apex, flat at the margin, rounded at the base, glabrous (at maturity), bearing below in a row on each side 3–4 impressed glands 3–9 mm from the margin, the lateral veins and larger cross-veinlets prominent below, obscure above; petiole 13–16 mm long, tomentose to glabrate, bearing 3–4 glands 1.5–2 mm in diameter, partially immersed in the thick petiole; stipules not seen. Inflorescence an axillary panicle 10–20 cm long, dark brown tomentose-velutinous, simple or compound, with the flowers ultimately borne in pseudoracemes 2–6 cm long containing 6–26 decussate flowers; floriferous bracts 1–1.5 mm long and wide, broadly triangular, bearing 2 prominent glands at the base, abaxially tomentose, persistent; peduncle none or occasionally up to 0.5 mm long; bracteoles like the bracts but smaller and eglandular. Pedicel (in fruit) ca 5 mm long, velutinous with a mixture of short T- and Y-shaped hairs, distally enlarged. Sepals (in fruit) 2.5 mm long, 2 mm wide, triangular, revolute at the apex, abaxially appressed-tomentose, adaxially glabrous, the anterior eglandular, the lateral 4 bearing 8 glands 1.8–2 mm long, elliptical, separated on the sepals. Petals and stamens unknown. Style bearing a short pedaliform apical-dorsal extension. Immature samaras up

to 36 mm long, widely spreading but the wings bent upward beyond the nut, scurfy-tomentose proximally; dorsal wing ca 30 mm long, 10 mm wide, straight or curved; nut 8–10 mm long, 4–5 mm high, without lateral crests or wings.

TYPE: BRAZIL. Amazônas: Lago do Castanho-Mirim, estrada da Petrobrás, mata virgem de terra firme, solo argiloso, humoso, meio úmido, 23 Jun 1973 imm fr, *Albuquerque, Coelho, & Mello 839* (INPA 39180, holotype; MICH, isotype).

Heteropterys marleneae belongs to the natural but difficult subgenus *Parabanisteria*, in which the sepals are always revolute at the apex. It will undoubtedly prove to have yellow petals like the rest of the subgenus. In that group it is unusual in having the short, distally enlarged pedicel sessile or subsessile. It is also notable for its compound inflorescence with dark brown, scurfy, tomentose-velutinous axes, and for the short persistent bracts and bracteoles, the bracts bearing two large glands. This distinctive and interesting species is named in honor of Dr. Marlene Freitas da Silva, Curator of the herbarium at INPA in Manaus. Under her careful supervision that collection has become one of the most important research herbaria in South America.

JANUSIA

All students of the Malpighiaceae have agreed that *Janusia* Adr. Jussieu and *Schwannia* Endlicher are closely related genera. They really differ only in these characters:

Stamens 6 (5 opposite the sepals plus 1 opposite the posterior petal); anthers densely tomentose; stout vines; cleistogamous flowers absent. *Schwannia.*

Stamens 5 (opposite the sepals) or fewer; anthers glabrous; slender vines; cleistogamous flowers present in 1 species. *Janusia.*

I have now encountered a new species that is perfectly intermediate between the two groups. It is generally very similar to *J. guaranitica* in habit and in possessing cleistogamous flowers, but it has six fertile stamens. Its anthers are sparsely hairy. It is therefore necessary to unite the two genera. The two generic names seem to have been published essentially simultaneously, i.e. both in April 1840 (Stafleu & Cowan, 1976; 1979), and they have never before been considered synonyms, so I must select one of the two names for the genus. I here choose *Janusia* Adr. Juss., for reasons that I shall discuss in some detail in my monograph of the genus. It is also necessary to select a lectotype for *Janusia*, and I here choose *Janusia guaranitica* (St. Hil.) Adr. Juss. Below are published several new combinations that are necessary when *Janusia* and *Schwannia* are combined, and the new intermediate species is described.

Janusia janusioides (Adr. Juss.) W. R. Anderson, comb. nov.
Fimbriaria janusioides Adr. Juss., Ann. Sci. Nat. 2° Sér. Bot. 13: 250. 1840.

Janusia lindmanii (Skottsberg) W. R. Anderson, comb. nov.
Schwannia lindmani Skottsberg, Kongl. Svenska Vetenskapsakad. Handl. 35(6): 29. 1901.

Janusia malmeana (Nied.) W. R. Anderson, comb. nov.
Schwannia malmeana Nied. in Engler, Pflanzenr. IV. 141: 540. 1928.

Janusia mediterranea (Vell.) W. R. Anderson, comb. nov.
Banisteria mediterranea Vell., Fl. Flum. 191 [text]. 1825 [1829, *fide* Carauta, 1973]; vol. 4 pl. 162 [atlas]. 1831.

This is surely an older name for the species widely known as *Schwannia elegans* (Adr. Juss.) Adr. Juss. Vellozo's description and figure leave little room for doubt as to its identity; note especially these features: six stamens, one style, red ciliate petals with white hairs, elongated white calyx glands, growing in inland thickets. I know of no other member of the Malpighiaceae that this could be.

Janusia schwannioides W. R. Anderson, sp. nov. Fig. 14.

Planta volubilis, caulibus gracilibus. Lamina foliorum majorum 3–4.4 cm longa, 1.3–2.2 cm lata, elliptica, basi plerumque rotundata, apice rotundata et apiculata, subtus prope basim 2 glandulis disciformibus stipitatis munita; petiolus 6–10 mm longus, eglandulosus. Flores chasmogami in umbellis axillaribus (2–) 3–4-floris portati; pedunculus 8–15 (–21) mm longus, apice vel paulo infra apicem bibracteolatus. Pedicellus 7–16 mm longus. Petala glabra, profunde laciniata, limbo 6–12.5 mm longo, 6–13 mm lato. Stamina 6, subaequalia; filamenta 4.5–6.5 mm longa, 3 sepalis anticis opposita libera, 3 sepalis posticis et petalo postico opposita ½–¾ connata; antherae 0.8–1.2 mm longae, paucipiliferae. Flores cleistogami 3 carpellis muniti. Samara basi rudimento alarum lateralium munita.

Vine with slender twining stems, forming thickets in shrubs to 3 m high; stems loosely sericeous to velutinous, glabrate in age, with an understory of thinner, shorter white hairs and an overstory of stiffer, longer golden hairs, these varying from strongly appressed to strongly spreading. Lamina of the larger leaves 3–5.2 cm long, 1.3–3 cm wide, elliptical or narrowly elliptical, mostly rounded and apiculate at the apex, slightly revolute at the margin, broadly cuneate or rounded at the base, sericeous above at first but soon glabrescent with some hairs persistent on the midrib, persistently sericeous, appressed-tomentose, or tomentose below, or belatedly glabrescent, bearing at or somewhat above the base below 2 stalked disciform glands 0.25–0.5 mm in diameter with stalks ca 0.3 mm long, the lateral veins and reticulum obscure on both sides; petiole 6–15 mm long, loosely sericeous to glabrate, eglandular, 0.4–0.5 mm in diameter; stipules 0.5–0.7 mm long, triangular, borne on stem at base of petiole. Chasmogamous and cleistogamous flowers both borne in axillary umbels or terminating short lateral shoots, produced simultaneously but mostly not in the same umbels. Chasmogamous flowers borne in umbels of (2–) 3–4 flowers, with a common stalk 5–25 mm long usually bearing 2 bracts or small leaves; floriferous bracts [subtending floriferous peduncles] 1–1.8 mm long, 0.3–0.5 mm wide, narrowly elliptical, membranous, glabrous or bearing a few hairs, eglandular; peduncle 8–15 (–21) mm long, 0.3–0.4 mm in diameter, loosely sericeous to glabrate; bracteoles like the bracts, appressed, usually borne at apex of peduncle, occasionally slightly below. Pedicel 7–16 mm long, loosely sericeous to glabrate except persistently sericeous at the apex, proximally slender like the peduncle but distally enlarged to 1 mm or more in diameter at the apex. Sepals 4–6 mm long, 1.5–2.7 mm wide, elliptical or obovate, rounded at the apex, thin, strongly incurved or inrolled in anthesis, bearing a few straight sessile hairs abaxially, ciliate on the margin at the apex, adaxially glabrous, the anterior eglandular and narrower, the lateral 4 biglandular, the glands green , 1.5–3 mm long, narrowly elliptical. Petals carrot-yellow, glabrous, deeply fimbriate-laciniate (the divisions at least 1 mm long), eglandular; 4 lateral petals widely spreading, with the claw 2.5–3.5 mm long, the limb flat and nearly circular or broadly cuneate at the base, 6–12.5 mm long, 6–13 mm wide; posterior petal with the thick claw erect, 3.3–4.5 mm long, the limb strongly reflexed, circular or obovate, 6–11 mm long, 6.5–12 mm wide. Stamens 6 (5 opposite the sepals plus 1 opposite the posterior petal), all fertile, subequal; filaments 5–6.5 mm long opposite sepals, 4.5–5.3 mm

FIG. 14. *Janusia schwannioides*. a) habit, × 0.5; b) base of lamina, abaxial side, to show hairs and glands, × 10; c) stipules, × 10; d) bud of chasmogamous flower, × 3; e) chasmogamous flower, × 2.5; f) androecium and gynoecium of chasmogamous flower, with anterior sepal to left and claw of posterior petal to right, 1 anterior-lateral sepal removed, × 5; g) anthers of chasmogamous flower, abaxial view (left) and adaxial view (right), × 15; h) cleistogamous flower, × 10; i) cleistogamous flower with samaras enlarging and sepals pulled back to show rudimentary petal, 2 stamens, and style, × 10; j) infructescence, with fruits all from cleistogamous flowers, × 0.5; k) fruit from a single cleistogamous flower, × 1.5; l) samara, × 1.5; m) embryo, × 5. Drawn by Karin Douthit from the type.

long opposite posterior petal, glabrous, the anterior 3 free, the posterior 3 one-half to three-fourths connate, all crowded around the style and curved downward toward the anterior sepal and then upward; anthers 0.8–1.2 mm long, alike, often reflexed, bearing a few appressed hairs on sides of locules and sometimes a tuft of longer, twisted hairs at apex or base. Carpels 1–1.5 mm high, borne on a low common receptacle, densely sericeous; style 1, borne on the anterior carpel, 5–6.5 mm long, glabrous, stout, lying in plane of symmetry of flower, curved downward toward anterior sepal and then abruptly upward at the apex, the terminal stigma often slightly oblique, extending just beyond the anthers. Cleistogamous flowers borne singly or, usually, in umbels of 2–4 flowers, with a common stalk 1–5 mm long; bracts and bracteoles like those of chasmogamous flowers but mostly shorter; peduncle 2–8 mm long; cleistogamous flowers occasionally replacing 2 of the 4 flowers in a chasmogamous umbel. Pedicel 3–8 mm long. Sepals 1.5 mm long, 0.7 mm wide, eglandular, appressed, narrowly elliptical, abaxially sparsely sericeous, adaxially glabrous. Rudimentary petals 1–5, 0.1–0.4 mm long, non-vascularized, concealed between bases of sepals. Stamens 2, opposite posterior-lateral sepals, with filaments 0.15–0.2 mm long and anthers 0.25–0.3 mm long, indehiscent. Gynoecium with all 3 carpels developed and fertile; style 1, borne on the anterior carpel, ca 1 mm long, hook-shaped, bent over between posterior carpels to bring stigma into contact with anthers. Fruit, whether derived from chasmogamous or cleistogamous flowers, comprising 3 samaras, or fewer through failure of 1 or 2 carpels to mature; samaras separating from a low, rounded or obscurely 3-sided torus 1 mm or less high; samara 18–20 mm long, loosely sericeous proximally; dorsal wing 12–15 mm long, 5.5–7 mm wide, with a rounded projection 1–2 mm high at the adaxial base; nut ca 2 mm high, 4 mm long, laterally flattened; lateral wings restricted to base of nut, partially to completely connate, forming an apparent flattened extension of the nut 2–3 mm long and wide at right angles to dorsal wing; cartilaginous carpophore well developed and functional, extending from receptacle down line of fusion of lateral wings. Embryo with the cotyledons subequal, flattened, folded back in the distal third.

TYPE: BRAZIL. Bahia: Trail from Lagoinha (which is 5 km SW of Delfino) to Minas do Mimoso (41°16′ W, 10°27′ S), elev 640 m, caatinga 1.5 km NW of Lagoinha, 7 Mar 1976 fl/fr, *Anderson 11748* (MBM, holotype; K, MICH, NY, RB, isotypes).

PARATYPES: BRAZIL. Bahia, Mun. Poções: 2.5 km W of Poções on road to Bom Jesus da Serra, dense roadside brush, Mar fl/fr, *Anderson 12514* (MICH, RFA); Km 10 da estrada que liga Poções (BR-116) ao povoado de Bom Jesus da Serra (ao W de Poções), transição entre Mata de Cipó e Caatinga, 750 m, Mar fl/imm fr, *Mori et al. 9517* (CEPEC, MICH).

Janusia schwannioides resembles *J. guaranitica* in its habit, inflorescence, samaras, and production of cleistogamous flowers, but in the latter species the petals are subentire, there are only five stamens, the stamens and style are ± erect and straight, and the cleistogamous flowers have only two carpels. The other species that resembles *J. schwannioides* is *J. janusioides sensu stricto.* It has shorter petioles, floriferous peduncles very short or absent, smaller flowers with the less deeply laciniate petals hairy adaxially on the claw, shorter, less curved androecium and gynoecium, and hairier anthers; it does not produce cleistogamous flowers.

MASCAGNIA

In the last volume of these Contributions (Anderson, 1980), I pointed out that *Banisteria riedeliana* Regel was an older name for *Mascagnia metallicolor*

Niedenzu, and made the appropriate new combination. Recently, while studying in Paris the types of species described by Adrien de Jussieu, I discovered that there are two still older names for this species. The new combination and a full synonymy for this species as I now understand it are given below. See the 1980 paper for a description and illustration of the species.

Mascagnia renidens (Adr. Jussieu) W. R. Anderson, comb. nov.
Hiraea renidens Adr. Jussieu, Ann. Sci. Nat. 2° Sér. Bot. 13: 26. 1840.
Hiraea heteropetala Adr. Jussieu, Arch. Mus. Hist. Nat. 3: 557–558. 1843.
Banisteria riedeliana Regel, Ind. Sem. Hort. Bot. Petropol. 17. 1855.
Tetrapterys renidens (Adr. Jussieu) Grisebach in Martius, Fl. Bras. 12(1): 88. 1858.
Tetrapterys heteropetala (Adr. Jussieu) Grisebach in Martius, Fl. Bras. 12(1): 88. 1858.
Mascagnia metallicolor Niedenzu, Arb. Bot. Inst. Lyc. 3: 20. 1908.
Mascagnia riedeliana (Regel) W. R. Anderson, Contr. Univ. Mich. Herb. 14: 21. 1980.

ACKNOWLEDGMENTS

My studies of the Malpighiaceae are currently supported by a grant from the National Science Foundation to The University of Michigan (DEB 81-03522); that grant is also helping to pay for this publication. I am most grateful to Dr. Alicia Lourteig, whose hospitality during the summer of 1981 made my lengthy visit at the Muséum National in Paris both pleasant and profitable. I extend my thanks also to Drs. Carmen Cristóbal, Antonio Krapovickas, T. Myndel Pedersen, Gert Hatschbach, and Paulo Occhioni for their friendly assistance during my recent visits to Argentina and Brazil, and to the many curators who sent specimens for my study as gifts or loans; their herbaria are represented by the following acronyms: BM, BR, C, CEPEC, CTES, F, G, GH, IAN, INPA, K, LA, LE, M, MBM, MG, MO, NY, P, R, RB, S, SP, U, UB, US, W. Karin Douthit drew the beautiful illustrations, with her usual combination of skill and attention to detail.

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ON *MEIOTHECIUM* (SEMATOPHYLLACEAE)

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The Sematophyllaceae are unusual among the pleurocarpous mosses in having many genera, most of which are mono- or oligotypic. Of approximately 53 genera, about 35 have four or fewer species. Often the genera are based on small peristomial differences, such as endostomial development. Some genera are separated on leaf papillosity differences, whereas other genera, such as *Acroporium,* permit this variation within a single species. The degree of alar development, which runs a full spectrum, is often the difference between two genera.

The Sematophyllaceae are a relatively recent family, as are most of the pleurocarps, probably derived from a Northern Hemisphere Hypnobryalean stock (Vitt, 1982). Thus, it is assumed that the Sematophyllaceae, a predominantly Southern Hemisphere family, migrated and radiated after continental drifting, which may explain the generic proliferation. Although there can be little doubt that some of the monotypic genera truly represent isolated endpoints of evolution, it is difficult to believe that two-thirds of the genera in the family fall into that category. The discrepancy is probably a result of both poor observation and a lack of understanding the values of morphological variation. The fact that most of the taxa occur in the tropics complicates the situation further because many tropical species are known only from type collections, which are often scanty or lacking mature sporophytes. The confusion is additionally compounded by some of the larger genera of Sematophyllaceae which are surely polyphyletic.

Meiothecium combines many of the problems outlined above. The genus is characterized by usually more or less ovate leaves with shortish cells; the alar cells are differentiated and somewhat inflated and colored, but not as extremely so as in many of the Sematophyllaceae. The capsules are erect to suberect, and the peristome is described as single with the exostome variously spaced and ornamented. Brotherus (1908) recognized and described three sections: *Eu-Meiothecium, Pterogonidiopsis* and *Pseudo-Meiothecium*. The three sections are separated mainly on the basis of sporophytic characters, although there is some gametophytic correlation. Section *Meiothecium,* containing the majority of species, is recognized by widely spaced, papillose exostome teeth. The calyptra is decidedly roughened at its apex. The section *Pterogonidiopsis*, with only a few South American species and a single African one, has the exostome teeth closely placed and ± smooth on the front surface except for prominent bars separating the individual plates. The calyptra is smooth. *Pseudo-Meiothecium* has plants more robust and an exostome whose teeth are closely placed. The ornamentation is described as papillose (Brotherus, 1908), but it is not like that of sect. *Meiothecium*. Rather, in sect. *Pseudo-Meiothecium* the papillae are arranged in tight horizontal rows, the type of sculpturing often seen in reduced hypnoid peristomes (Buck, 1980). The four species (all of northern South America) have smooth calyptrae.

Pterogoniella first appeared in the literature as a Schimper name "in herb. Mus. Par." (Jaeger, 1877) in a catalogue with no description but with 33 species listed under it. In 1894 Brotherus described two new African species in the genus, *P. usambarica* and *P. stuhlmannii*, even though the genus had still not been described nor had any indication been given in the literature as to how Schimper himself circumscribed it. In 1897 Brotherus described another African species, *P. chloroclada*. It is obvious that at this time Brotherus had no intention of describing *Pterogoniella* as a new genus. However, both Wijk et al. (1967) and Farr et al. (1979) recognized *P. chloroclada* as a *descriptio generico-specifica*. In 1908 Brotherus placed *Pterogoniella* in synonymy under *Meiothecium*. Both *P. usambarica* and *P. chloroclada* were transferred to *Meiothecium; P. stuhlmannii* was transferred to *Rhaphidostegium* (≡ *Sematophyllum*).

Very similar to *Meiothecium* is *Meiotheciopsis*. *Meiotheciopsis* supposedly differs from *Meiothecium* by a double peristome and from the sect. *Pterogonidiopsis* by the exostome teeth more strongly barred on the front surface.

An examination of almost all South American taxa of *Meiothecium*, as well as a representative selection of Old World species, indicates that the genus is polyphyletic. *Meiothecium*, described from Samoa (Mitten, 1868), is easily circumscribed sporophytically. The peristome of widely spaced, narrow, non-bordered, papillose exostome teeth and no endostome is surprisingly constant across the broad range of gametophytic variation. However, careful dissection of mature capsules indicates that the species of sections *Pterogonidiopsis* and *Pseudo-Meiothecium* not only have very different exostomes, but also have reduced endostomes. At times the segments can even be seen with a dissecting microscope projecting straight up between the recurved teeth.

In the New World there seem to be only two true species of *Meiothecium*: *M. boryanum* (C. Müll.) Mitt. (syn. *M. scabriusculum* Besch. and *M. wrightii* (C. Müll.) Broth.) from the West Indies and *M. revolubile* Mitt. of Amazonian campinas.

As noted above, the section *Pterogonidiopsis* is very close to *Meiotheciopsis*. The supposed differences in the peristomial development in *Meiotheciopsis* (including the presence of an endostome and the more strongly barred exostome) are based on a poor understanding of sect. Pterogonidiopsis. A comparison of the peristomes of *Meiotheciopsis lageniformis* (C. Müll.) Broth. and *Meiothecium commutatum* (C. Müll.) Broth., reveals that they are very similar, with the endostome of *M. commutatum* only somewhat more reduced. Gametophytically the plants are also similar. Because of the resemblances a congeneric alliance is appropriate.

Meiotheciopsis commutata (C. Müll.) Buck, comb. nov.

Neckera commutata C. Müll., Bot. Zeit. (Berlin) 15: 385. 1857.

Pterogoniella commutata (C. Müll.) Jaeg., Ber. Tät. St. Gall. Naturw. Ges. 1875–76: 211. 1877, comb. inval.

Meiothecium tenerum Mitt., J. Linn. Soc. London, Bot. 12: 470. 1869, syn. nov.

Meiotheciopsis usambarica (Broth.) Buck, comb. nov.

Pterogoniella usambarica Broth., Bot. Jahrb. Syst. 20: 208. 1894, nom. inval.

Meiothecium usambaricum Broth., Nat. Pfl. 1(3): 1101. 1908.

Meiotheciopsis laxiuscula (Card.) Buck, comb. nov.

Pterogoniella laxiuscula Card., Rev. Bryol. 36: 51. 1909.

Meiotheciopsis longidens (Ångstr.) Buck, comb. nov.

Potamium longidens Ångstr., Öfv. Förh. K. Sv. Vet.-Akad. 33(4): 41. 1876.

Pterogonium longidens C. Müll. ex Ångstr., loc. cit., nom. nud. in syn.

Pterogoniella longidens (Ångstr.) Jaeg., Ber. Tät. St. Gall. Naturw. Ges. 1875–76: 211. 1877, comb. inval.

Meiothecium longidens (Ångstr.) Broth., Nat. Pfl. 1(3): 1101. 1908.

Meiotheciopsis lagenifera (Mitt.) Buck, comb. nov.

Meiothecium lageniferum Mitt., J. Linn. Soc. London, Bot. 12: 470. 1869.

Pterogoniella lagenifera (Mitt.) Jaeg., Ber. Tät. St. Gall. Naturw. Ges. 1875–76: 207. 1877, comb. inval.

Meiotheciopsis is probably most closely related to *Schraderella* of Venezuela. Type material of the sole species, *S. pungens* C. Müll., at NY has no peristome, but based on the illustration in Brotherus (1908) it (presumably) differs in the absence of an endostome and exostome teeth paired.

Meiothecium sect. *Pseudo-Meiothecium* has a reduced hypnoid exostome and a fairly conspicuous endostome. The leaf cells are often short, but in some species they are linear. The species assigned to this section are not related to either *Meiothecium* s.str. or *Meiotheciopsis*. Rather, they seem most closely related to *Sematophyllum caespitosum* (Hedw.) Mitt. and its allies. The group is characterized by mostly ovate, short-pointed leaves with relatively short leaf cells. The setae are short, and the capsules are mostly erect. The peristome is scarcely reduced. Although widespread, *S. caespitosum* should not be interpreted as widely as Dixon (1920) suggested. Leaf shape and areolation appear constant.

The following combinations are thus proposed:

Sematophyllum aptychoides (C. Müll.) Buck, comb. nov.

Neckera aptychoides Schlieph. ex. C. Müll., Bot. Zeit. (Berlin) 15: 382. 1857.

Meiothecium aptychoides (C. Müll.) Mitt., J. Linn. Soc. London, Bot. 12: 471. 1869.

Pterogoniella aptychoides (C. Müll.) Jaeg., Ber. Tät. St. Gall. Naturw. Ges. 1875–76: 209. 1877, comb. inval.

Meiothecium sulcatum Mitt., J. Linn. Soc. London, Bot. 12: 470. 1869, syn. nov.

Sematophyllum fabronia (Besch.) Buck, comb. nov.

Meiothecium fabronia Besch., J. Bot. (Morot) 5: 343. 1891.

Pterogoniella fabronia (Besch.) Par., Ind. Bryol. 1047. 1898, comb. inval.

Sematophyllum negrense (Mitt.) Buck, comb. nov.

Meiothecium negrense Spruce ex Mitt., J. Linn. Soc. London, Bot. 12: 471. 1869.

Pterogoniella negrensis (Mitt.) Jaeg., Ber. Tät. St. Gall. Naturw. Ges. 1875–76: 209. 1877, comb. inval.

Sematophyllum mittenianum Buck, nom. nov.

Meiothecium andinum Mitt., J. Linn. Soc. Bot. 12: 470. 1869 non *Sematophyllum andinum* Mitt., op. cit. 483.

It may be possible to segregate *Sematophyllum caespitosum* and closely related species generically. The short leaf cells and short setae with erect capsules are distinctive in *Sematophyllum*. However, until this large, widespread genus is better known it seems best to retain it in a catch-all genus.

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THE NORTH AMERICAN DISTRIBUTION OF THE GENUS *DRYOPTERIS*

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INTRODUCTION

The Woodferns, *Dryopteris*, are conspicuous, well collected ferns of mainly forests and swamps that occur over most of North America except the Great Plains. They become rare and sporadic in southwestern United States and in southern Florida. The 15 sexual taxa display a diverse array of mainly temperate, boreal, and arctic distribution patterns that appear to have been greatly influenced by Pleistocene glaciations. These patterns contribute toward an understanding of the complex phylogenetic relationships of these plants. There are nine diploid taxa and six polyploid taxa. Comparisons of possibly related Old World species provides insight into past distributions and migration patterns. Five of the polyploids are perhaps the most interesting in terms of glacial history; three of these grow exclusively in eastern North America. Glaciation may have played a major role in the origins of these allopolyploids by creating conditions conducive to hybridization. Two other allopolyploid Woodferns have amphi-Atlantic distributions, and Wagner (1971) proposed that they may have had a common parent (SS), now presumably extinct. As will be seen, similarities between the ranges of these two ferns support this suggestion.

The first comprehensive treatment of the overall geography of ferns was by Christ (1910). However, there are few in-depth studies (Smith, 1972; Tyron, 1969, 1970, 1971; Wagner & Wagner, 1965).

MATERIALS AND METHODS

The ranges are plotted of 13 of the 15 sexual taxa of *Dryopteris* occurring in North America, north of Mexico (including the two primarily Mexican taxa whose ranges barely extend into the southwest United States). Some of the distribution maps include localities in Iceland, a land mass often considered to be part of the Old World. The square symbols on the maps (Figs. 1, 3, 6, 8–19) represent herbarium specimens that we both examined and annotated. The dots represent localities learned from reliable literature or through correspondence with other pteridologists. Many of the specimens represented by dots were also seen by Wagner.

RESULTS

Dryopteris fragrans (L.) Schott (Fragrant fern) is a diploid that prefers shaded or exposed and usually north facing cliffs (Wherry, 1961; Carlson, 1979). Its

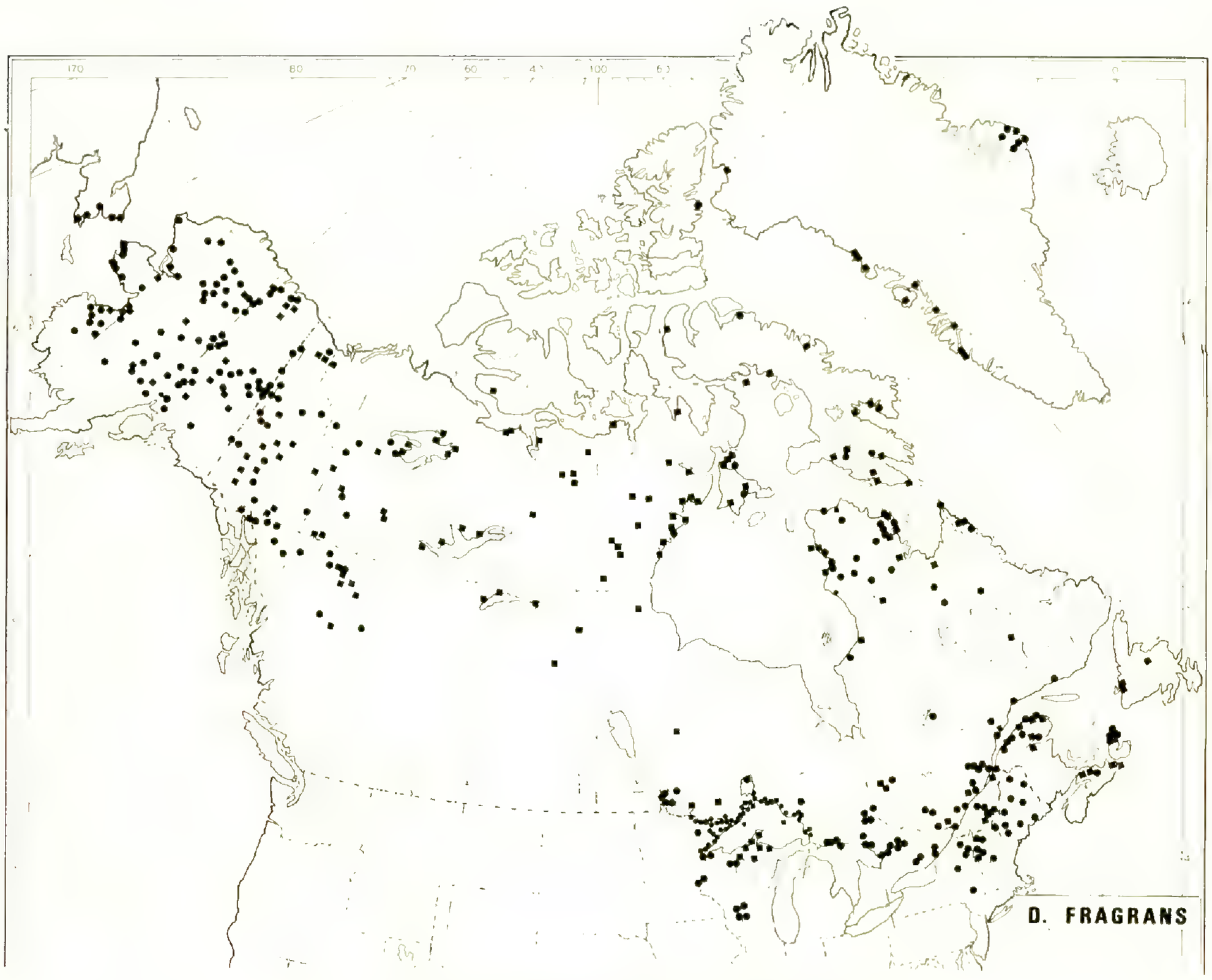

FIG. 1. *Dryopteris fragrans* range in North America.

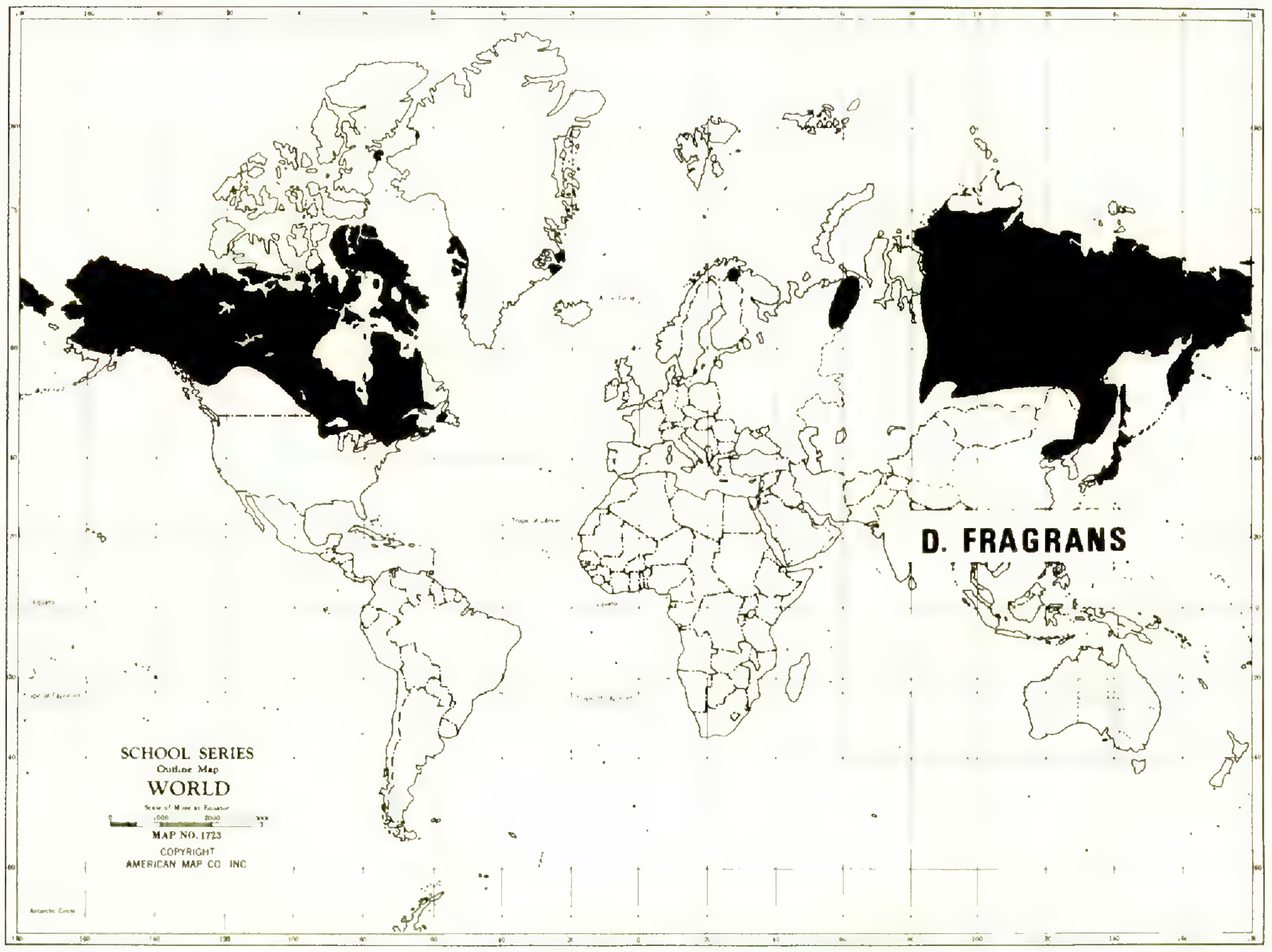

FIG. 2. *Dryopteris fragrans* approximate global range.

circumboreal-arctic range extends in northern latitudes through North America (Fig. 1) and across northern Asia and Siberia and southward into China, Korea, and Japan (Fig. 2), with disjunct populations in northern Finland and northwest Russia.

The circumboreal *Dryopteris filix-mas* (L.) Schott (male fern) is a tetrapoloid. Its taxonomy in North America is poorly understood. It may be an autopoly-

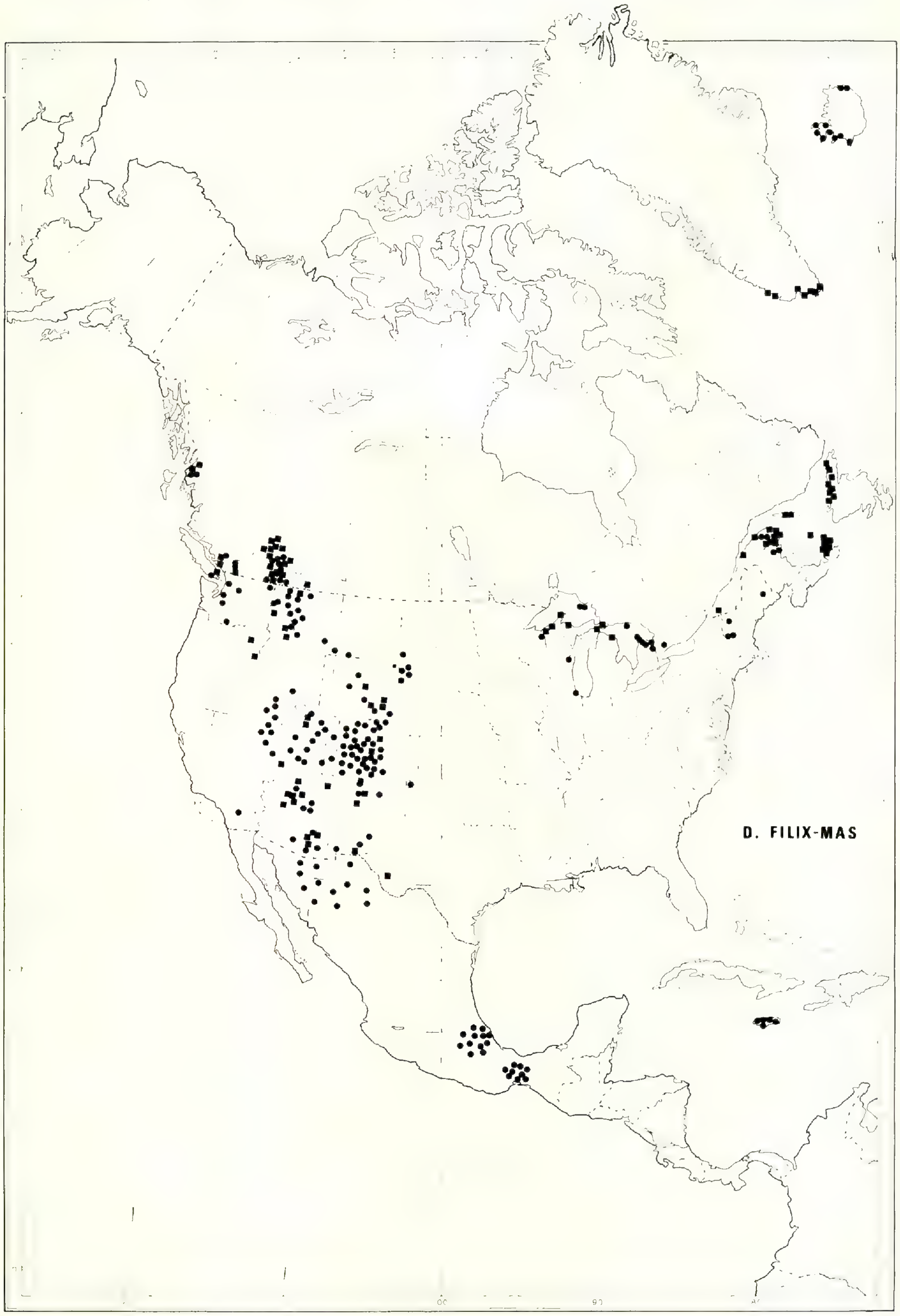

FIG. 3. *Dryopteris filix-mas* range in North America.

ploid (Wagner, 1971) or an allopolyploid (Britton, pers. comm.). It occurs in mountainous regions or in areas with exposed bedrock and/or talus slopes (Carlson, 1979) in most parts of its North American range (Fig. 3). In the west *D. filix-mas* extends through the Rocky Mountains from British Columbia to northern Mexico. Male fern also has a disjunct population in the San Bernadino Mountains in southern California. In eastern North America *D. filix-mas* is scattered from the Great Lakes to Greenland and Iceland.

Dryopteris arguta (Kaulf.) Watt (Coastal Woodfern), a diploid of rocky ravines and partially shaded slopes (Grillos, 1966), has a Cordilleron range extending along the west coast of North America from northern Baja Calfornia to southern British Columbia. It also has populations in the High Sierras of California as well as disjunct populations in the mountains of south-central Arizona in Pimal and Gila counties.

Jermy (*in litt.*, 1979) stated that when he examined specimens of this species from the University of California (Berkeley) herbarium, what appeared to be two distinct spore sizes were found. He suggested that the western American *D. arguta* may contain a tetraploid cytotype as well as the known diploid. Another variable character is broad and narrow frond forms. There are three frond types (narrow, normal and broad) (Fig.'s 4A, 4B, 4C). As illustrated (Fig. 5), the range of the narrow form is restricted to the High Sierras of California, while the broad form occurs on Santa Catalina and Santa Cruz Islands and along with one locality in Humboldt Co., California. The normal form grows predominantly along the coast but its range also overlaps with those of the narrow and broad forms. The two extreme forms may only be environmentally induced variations of *D. arguta* produced by local conditions.

Dryopteris expansa (Presl) Frazer-Jenkins (Spreading Woodfern), best known in previous botanical literature as *D. dilatata* (Hoffm.) Gray or *D. assimilis* S. Walker is a diploid of cool talus slopes and swamps, mainly in woodlands (Carlson, 1979). It exhibits an amphioceanic distribution pattern (Fig. 7) with populations in north temperate and sub-boreal eastern and western North America (Fig. 6), Europe, and eastern Asia.

Much confusion has existed regarding the North American range of Spreading Woodfern because it has been lumped with other species in the *D. carthusiana*

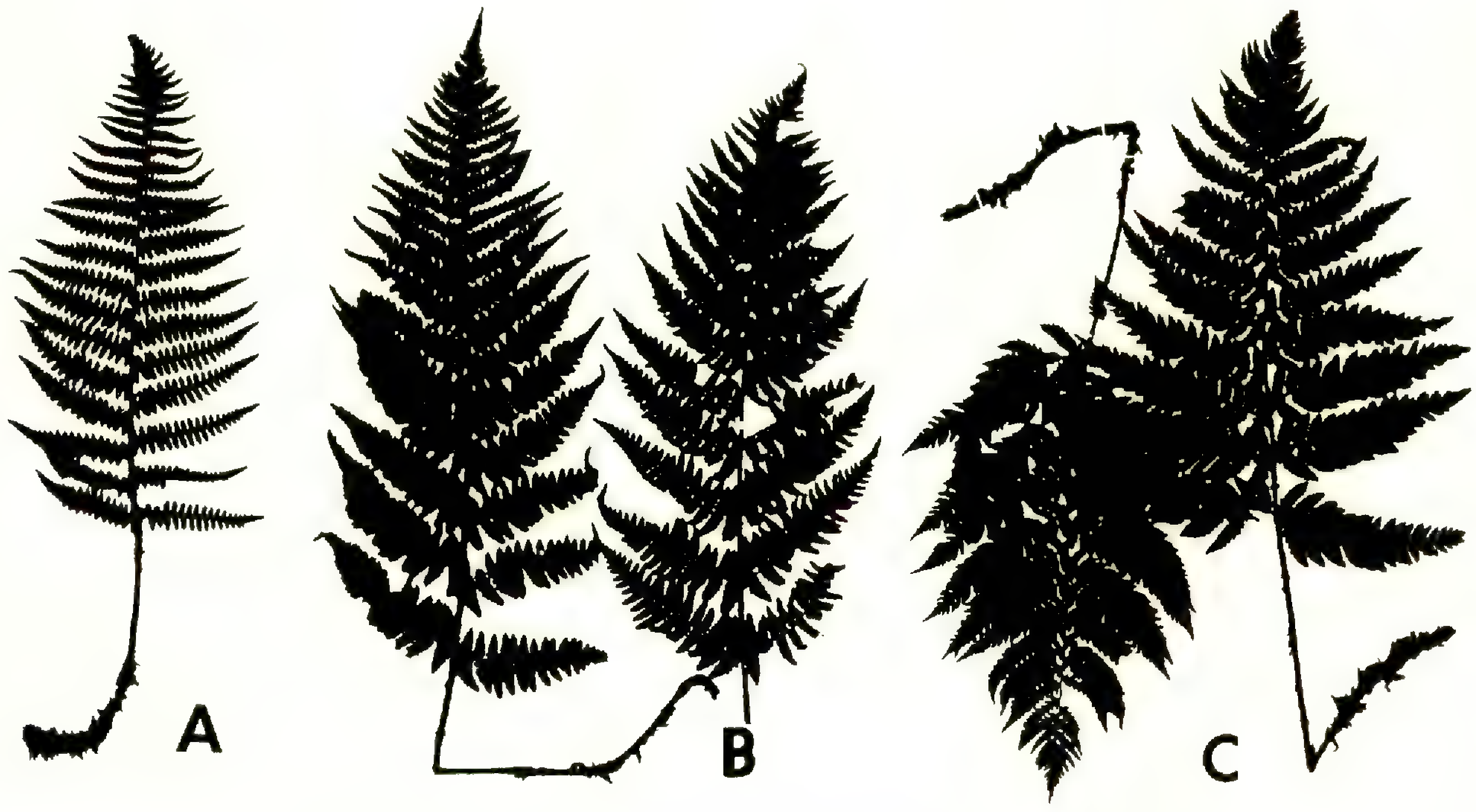

FIG. 4. *Dryopteris arguta*: silhouettes of herbarium specimens.

complex, which have collectively been called *D. austriaca* (Jacq.) Woynar (often also referred to as *D. dilatata*). For example, Hultén (1968) illustrated the range of *D. austriaca* as continuous between the Pacific and Atlantic oceans across Canada. However, careful examination and revision of western Canadian *Dryopteris* herbarium specimens an the subsequent mapping of their localities results in a pattern (Fig. 6) that supports Britton's (1972) suggestion that in western Canada the range of the Spreading Woodfern extends only as far east as western Alberta. *D. expansa* has also been confused with the allotetraploid *D. campyloptera* Clarkson (Mountain Woodfern) of eastern North America.

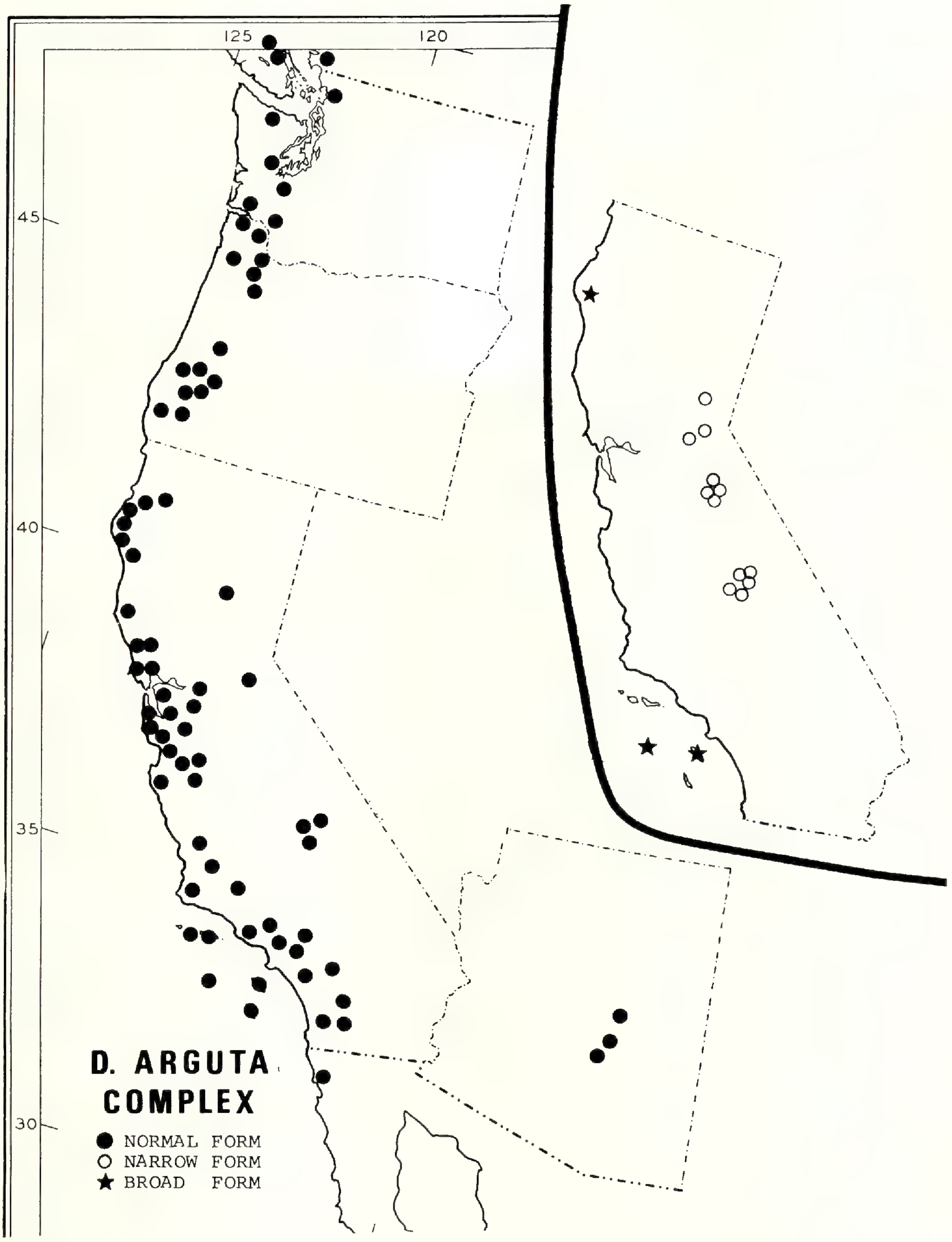

FIG. 5. *Dryopteris arguta* range.

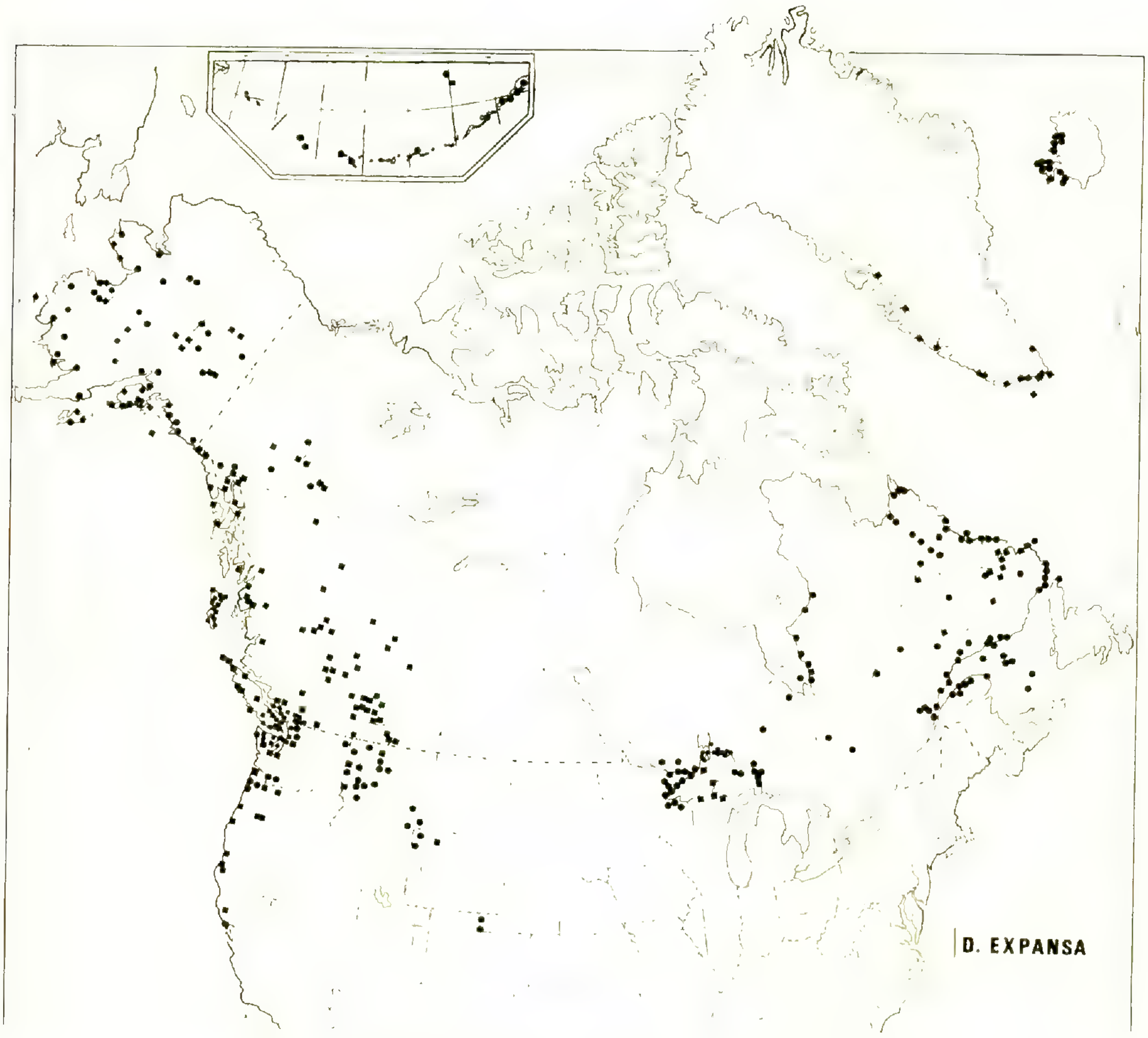

FIG. 6. *Dryopteris expansa* range in North America.

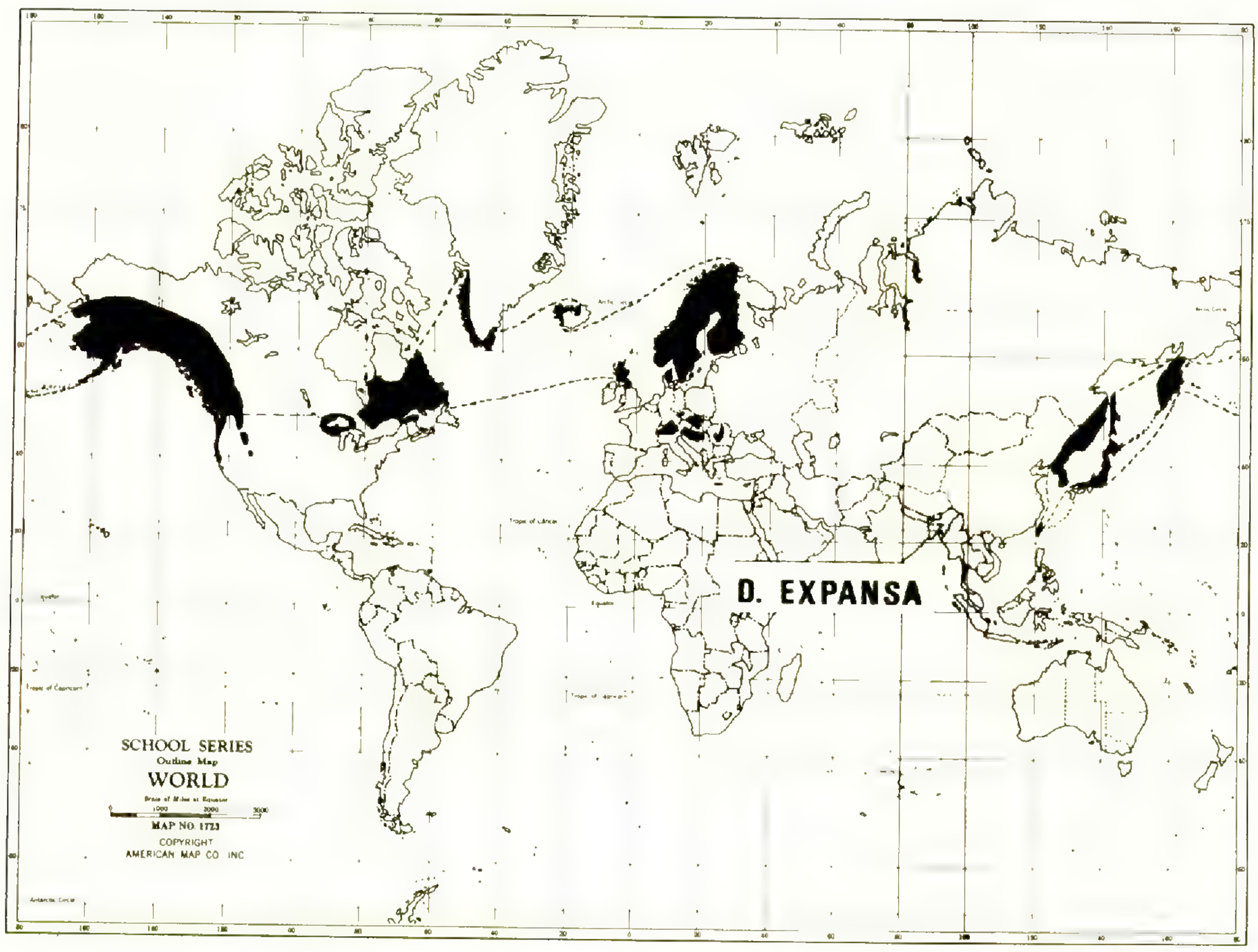

FIG. 7. *Dryopteris expansa* approximate global range.

Four diploid Woodferns have ranges restricted to eastern North America. The two most common are *Dryopteris intermedia* (Muhl.) Gray (Glandular Woodfern, Florist Fern) and *D. marginalis* (L.) Gray (Marginal Woodfern). *D. intermedia* grows predominantly in rich woods while *D. marginalis* prefers drier more upland forests, particularly ones with rocky slopes (Wherry, 1961; Carlson, 1979). *D. intermedia* extends (Fig. 8) southward through the Appalachian Mountains into northern Georgia and Alabama and westward into eastern Missouri, central Iowa and northern Minnesota. In Canada it grows along the Great Lakes and the St. Lawrence Seaway, in Newfoundland, Nova Scotia, New Brunswick, southern Quebec and southeastern Ontario. The northern part of the range of *D. marginalis* (Fig. 9) is very similar to that of *D. intermedia* but it does not extend into Minnesota. However, the south Marginal Woodfern extends much farther west through the Plains states of Missouri, Arkansas, Nebraska and Oklahoma, perhaps because it tolerates drier habitats than does the Grandular Woodfern.

Dryopteris goldiana (Hooker) Gray (Goldie's Woodfern), a fern of extremely rich mesic woodland habitats (Wherry, 1961; Carlson, 1979), is another diploid Woodfern that is restricted to eastern North America, but it is considerably less common and its range (Fig. 10) is smaller than that of *D. intermedia* or *D. marginalis*, presumably because its habitat is much more specific. The southern bound-

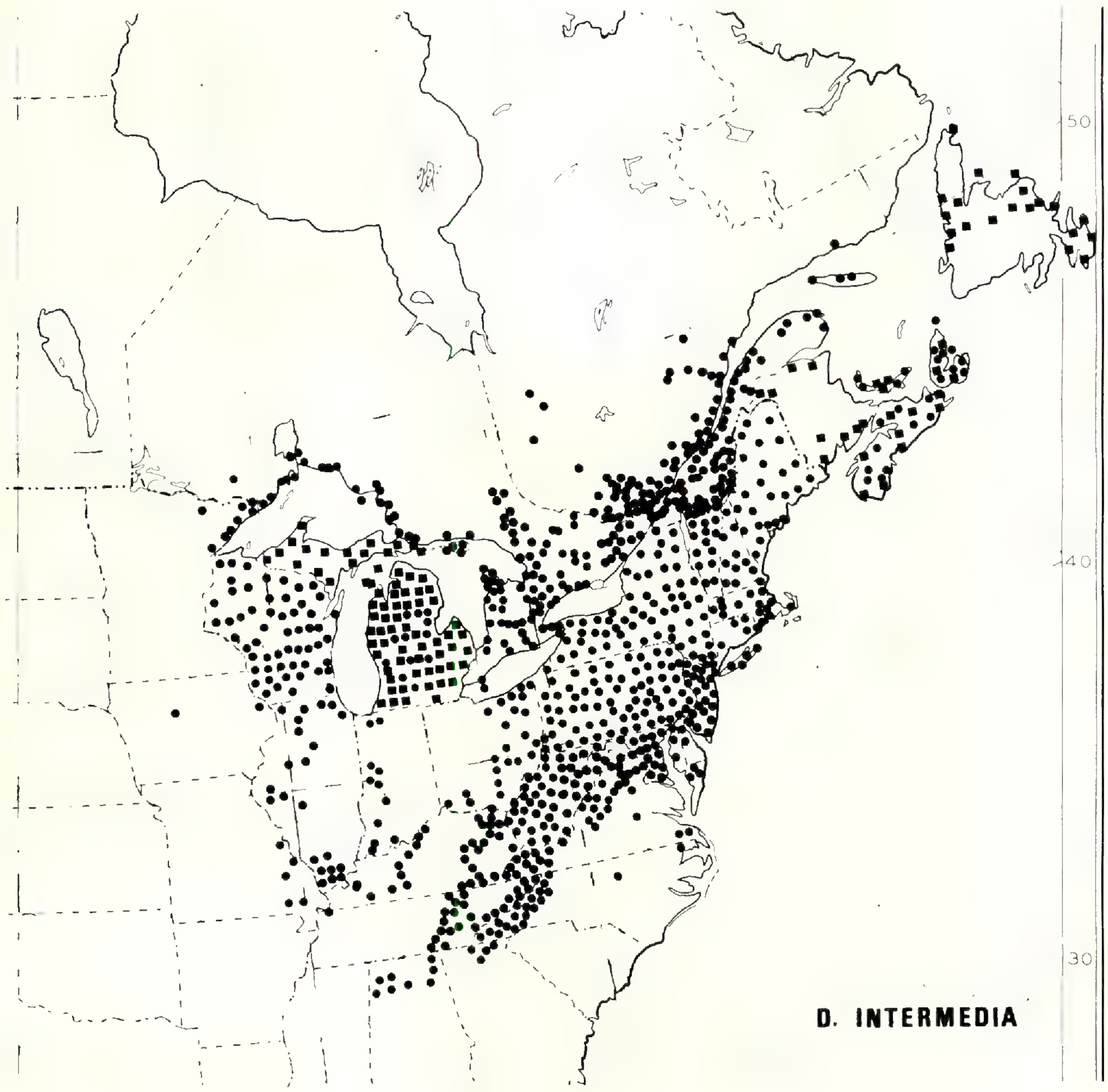

FIG. 8. *Dryopteris intermedia* range.

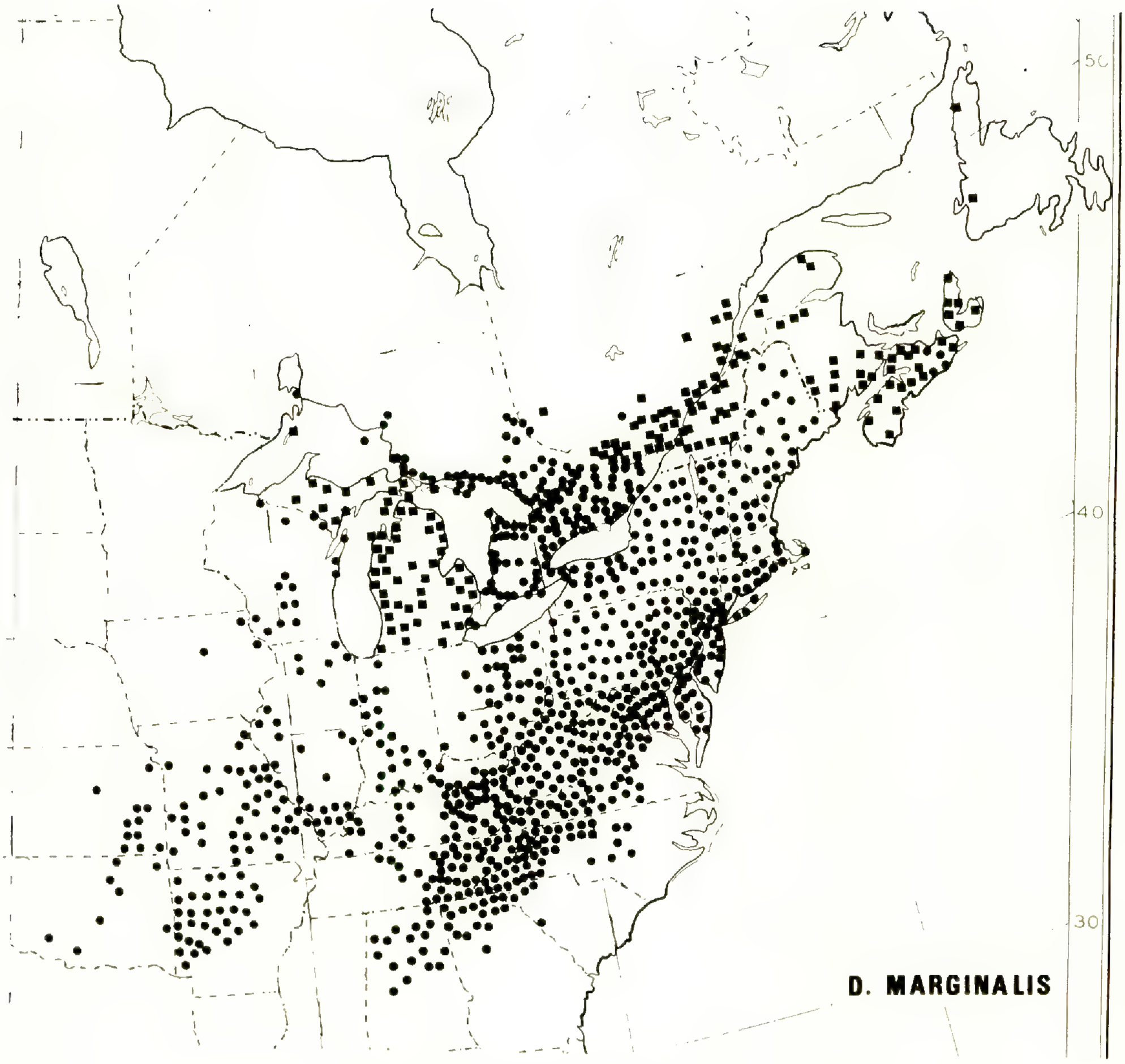

FIG. 9. *Dryopteris marginalis* range.

aries of its range are similar to those of *D. intermedia* but it does not extend so far north; it reaches only southeast Ontario and southwest Quebec. *D. goldiana* does, however, extend farther west into Missouri than *D. intermedia*.

Dryopteris ludoviciana (Kze.) Small (Florida Woodfern), is a diploid whose distribution (Fig. 11) is restricted to damp woods and swamps and rocky ledges in hammocks (Wherry, 1972) on the coastal plain and the lower piedmont of the United States from North Carolina to Florida and west to Louisiana. It does however, extend up into the Cumberland plateau in Alabama.

Dryopteris celsa (Palmer) Small (*D. goldiana* × *ludoviciana*) (Log Fern) is an endemic allotetraploid which grows on rich hummocks and on rotting logs in swamps (Carlson, 1979). The present distribution of the Log Fern (Fig. 12) extends south from New Jersey to northern South Carolina and northern Alabama and west to northern Louisiana and western Arkansas. The range has two interesting disjunct areas, namely the vicinity of Rochester, New York region and southwestern Michigan. Disjunct populations of *Woodwardia areolata* (L.) Moore (Netted Chain-fern) and *Lygodium palmatum* (Bernh.) Sw. (Climbing Fern) are also known from southwestern Michigan. Several new localities for *D. celsa* have been found in recent years including additional localities in four southwestern Michigan counties, and a specimen from Missouri originally thought to be *D. clintoniana* (Eaton) Underwood (Clinton's Fern) was determined by us to be

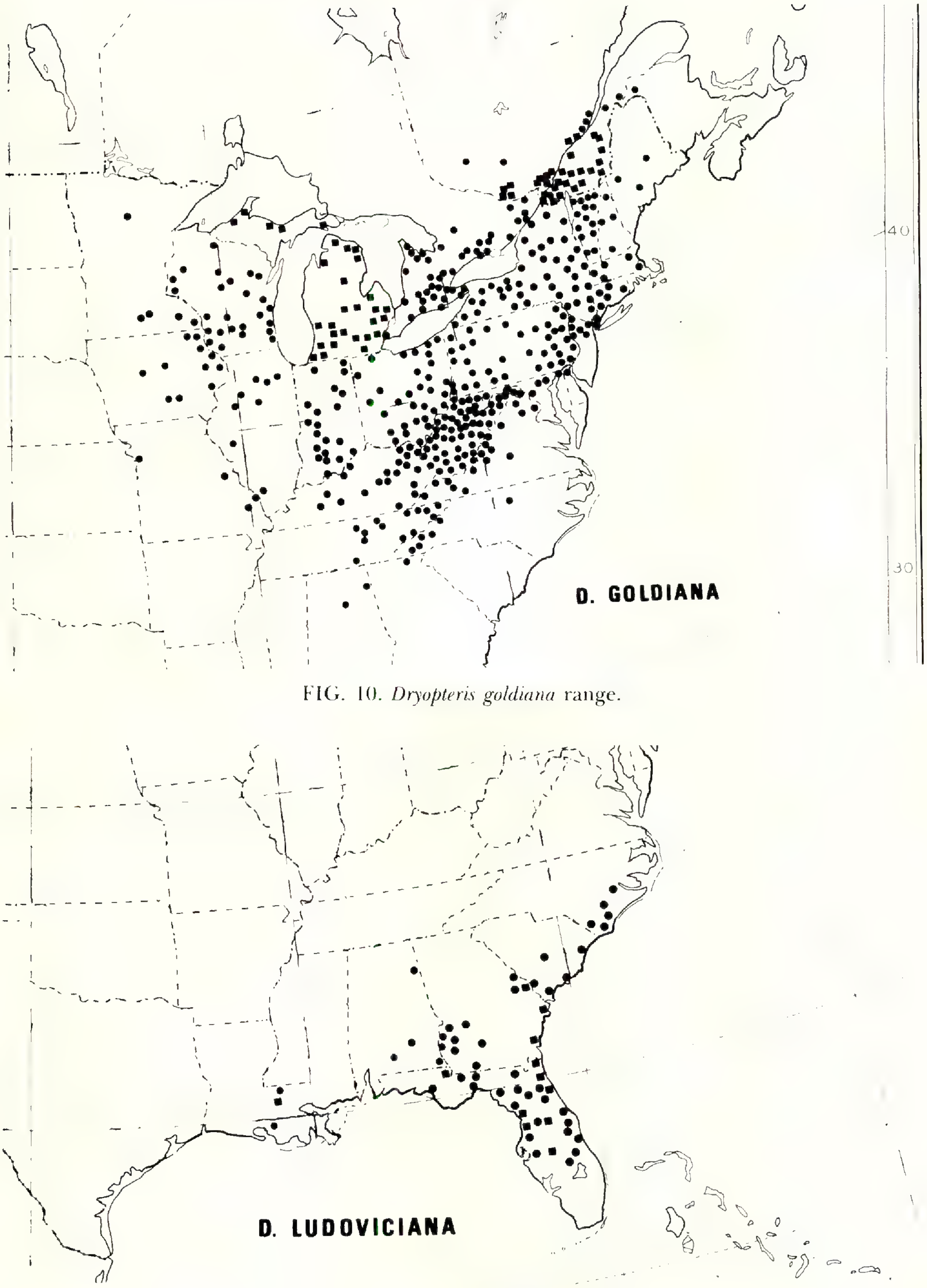

FIG. 10. *Dryopteris goldiana* range.

FIG. 11. *Dryopteris ludoviciana* range.

D. celsa. Single localities were also recently verified in both Illinois and Indiana, firsts for both states. Due to the morphological similarity between *D. celsa* and *D. clintoniana* 1, many *D. celsa* collections have been misidentified as *D. clintoniana*. As these mistakes are corrected, the known records of *D. celsa* may increase, particularly in the northern part of its range between its presently known disjunct populations and the major area of its assumed range.

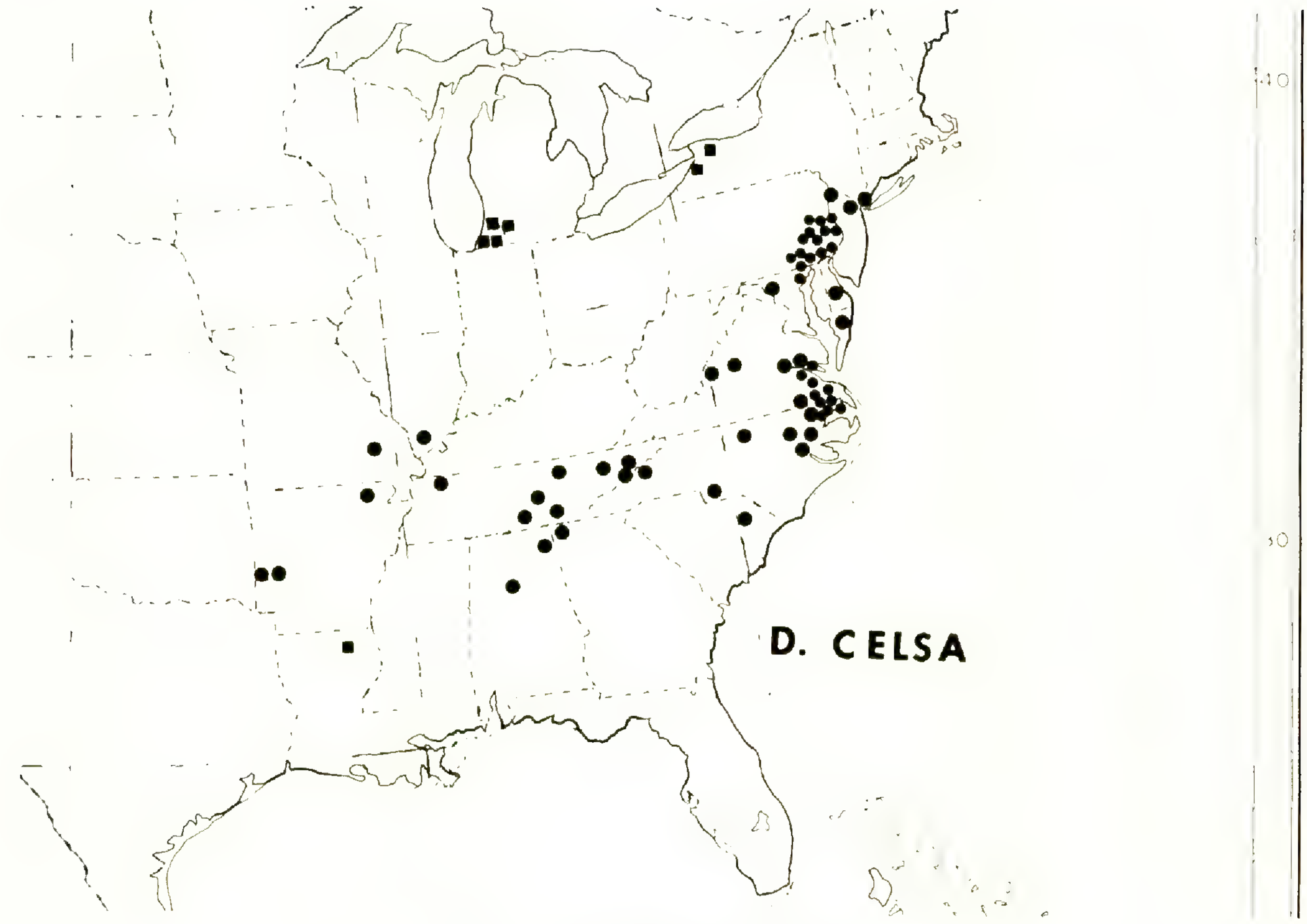

FIG. 12. *Dryopteris celsa* range.

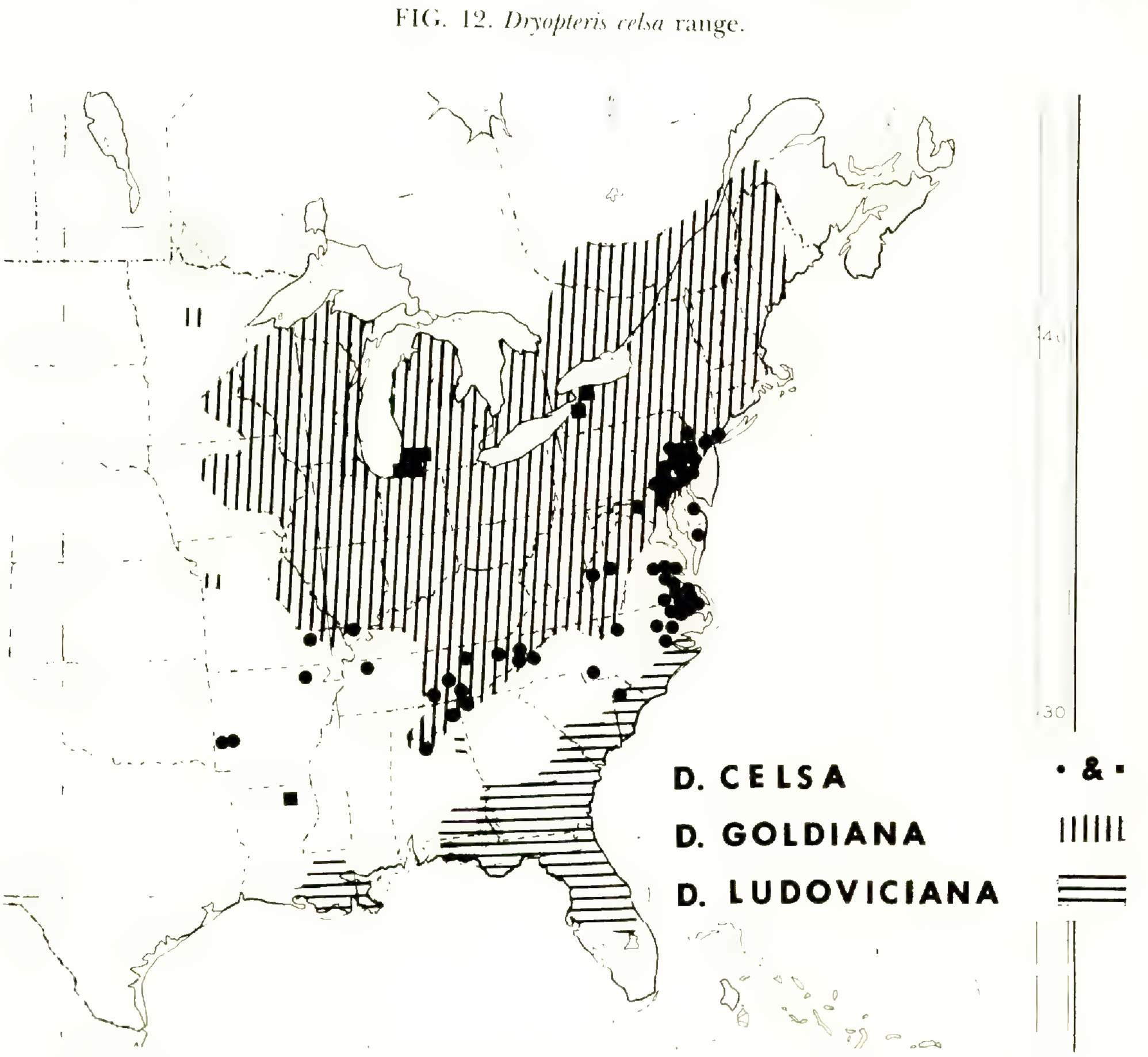

FIG. 13. *Dryopteris celsa* range with ranges of its parents (*D. goldiana* & *D. ludoviciana*).

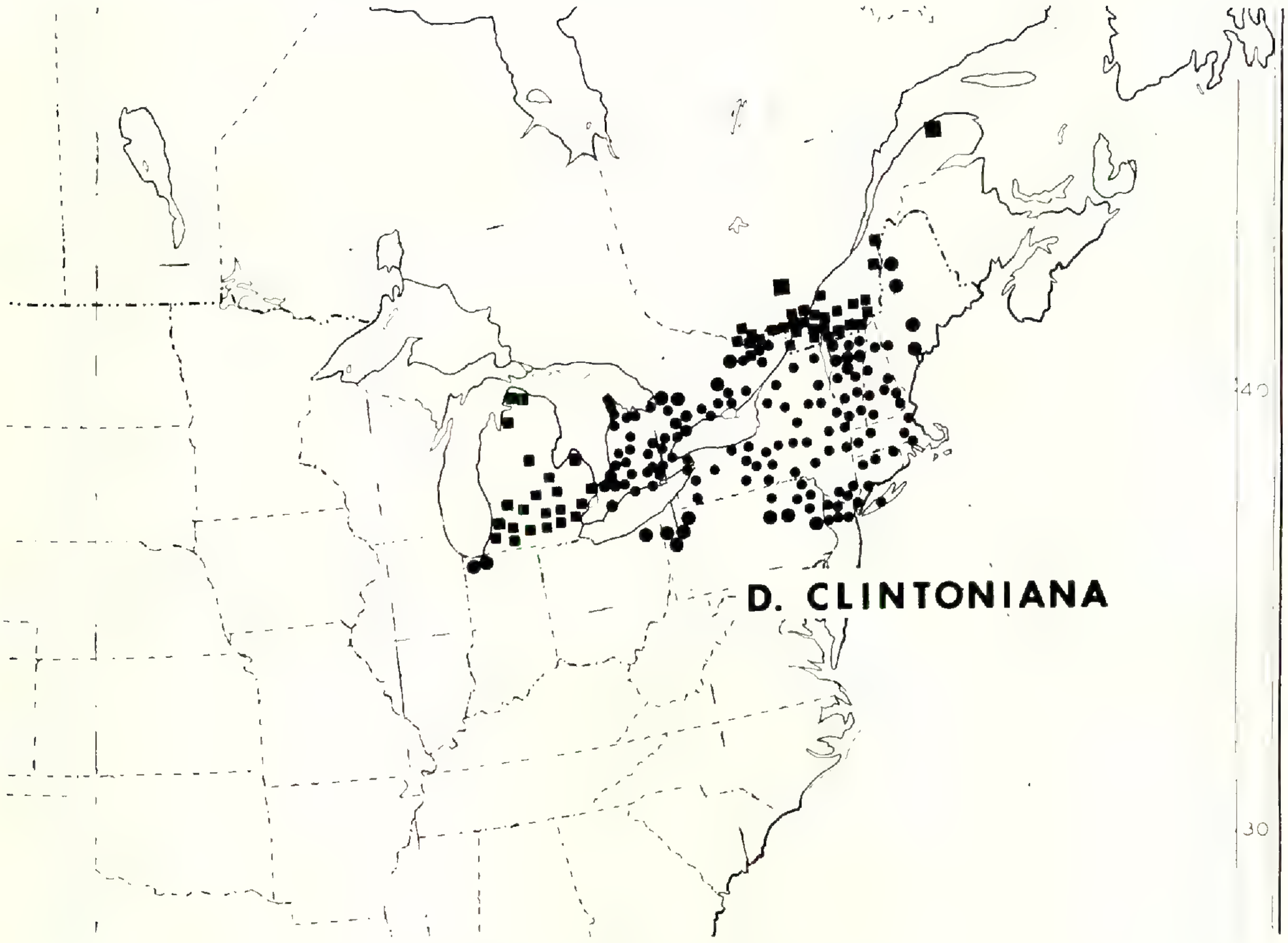

FIG. 14. *Dryopteris clintoniana* range.

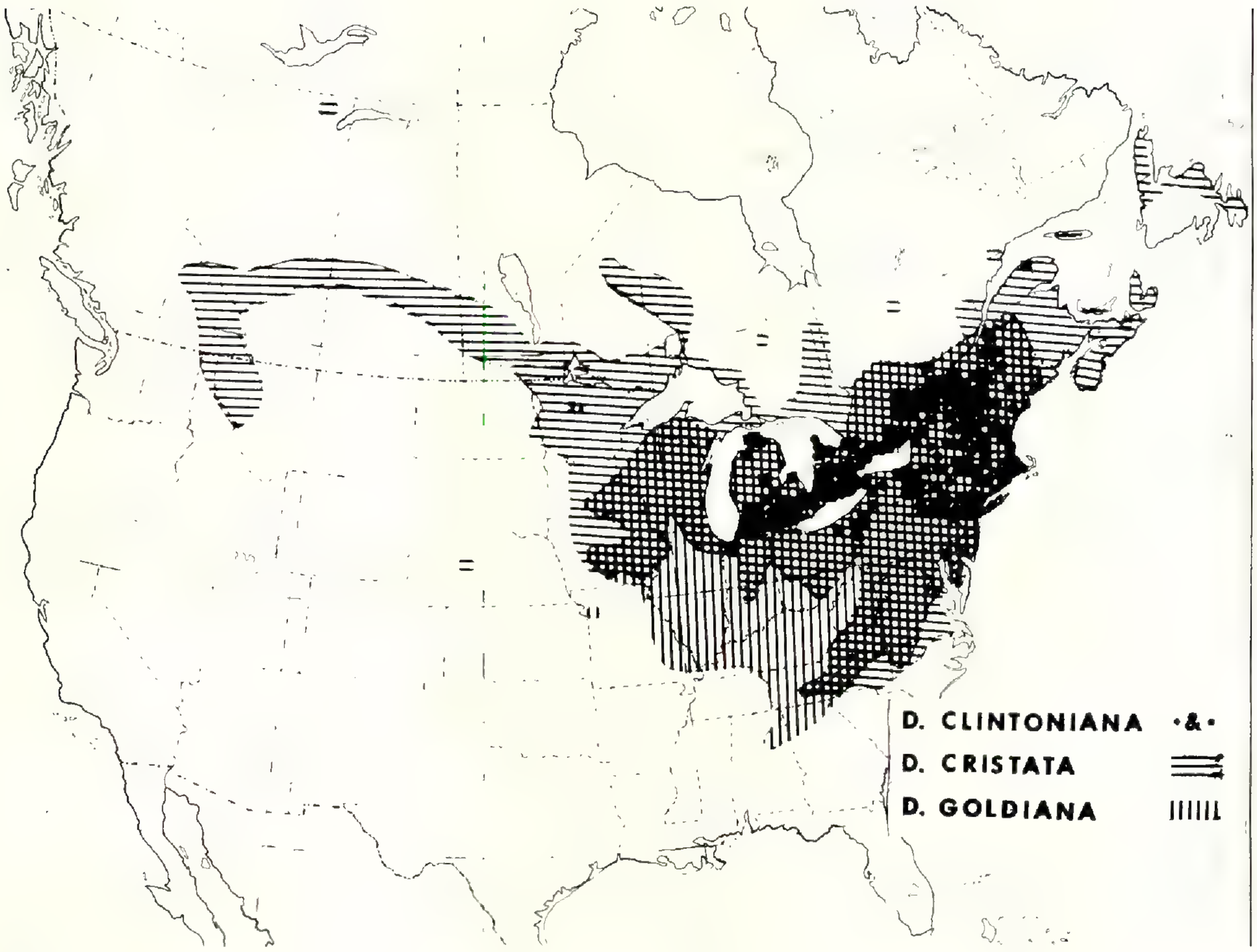

FIG. 15. *Dryopteris clintoniana* range with ranges of its parents (*D. cristata* & *D. goldiana*).

These misidentifications have also led people to believe that the range of *Dryopteris clintoniana* (*D. cristana* × *goldiana*), a North American allohexaploid, extends much farther south than it actually does. Montgomery (1976) showed that in New Jersey *D. clintoniana* does not reach below the glacial border. The southern boundary of its range (Fig. 14) in Pennsylvania and New York also follows the southern boundary of the ice sheet advance. It has populations in northeast Ohio, northwest Indiana and much of the Lower Peninsula of Michigan. Its range in Canada is similar to that of one of its parents (*D. goldiana*) (Fig. 10) since it grows in [southern] southeast Ontario, [southern] southwest Quebec, in addition to a single known locality on the Gaspe Peninsula.

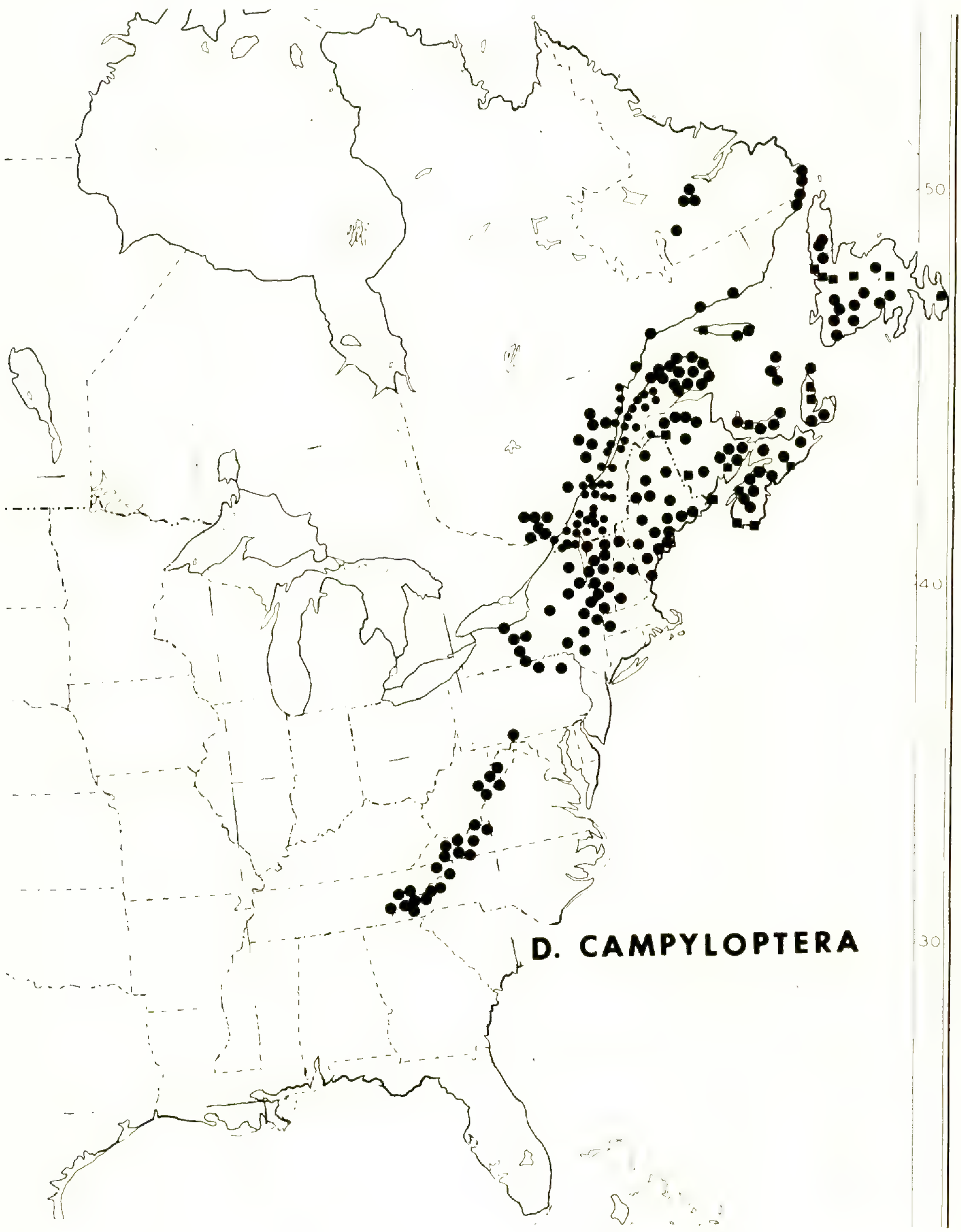

FIG. 16. *Dryopteris campyloptera* range.

Dryopteris campyloptera is an endemic allotetraploid whose parents are *D. expansa* and *D. intermedia* (Wagner and Hagenah, 1962; Wagner, 1963; Wagner, 1971; Gibby, 1977). Its distribution (Fig. 16) extends into southeastern Canada as far north as Labrador and southward down the Appalachians through the United States to Tennessee and North Carolina.

The two allotetraploid species, *Dryopteris cristata* (L.) Gray (Crested Woodfern) and *D. carthusiana* (Vill.) H. P. Fuchs (syn. *D. spinulosa* (Muell.) Watt) (Spinulose Woodfern) have amphi-Atlantic ranges. Because of their similar distributions, their ranges are described together. Both *D. cristata* and *D. carthusiana* are common throughout the Great Lakes region and in New England. Their ranges (Figs. 18 & 19) extend as far west as eastern North Dakota, and both have disjunct poulations in the same region in western Nebraska. The southern boundary of the range of *D. cristata* runs through southern Iowa, northern Illinois, southern Indiana and southern Ohio. In the Appalachians it occurs further south, being known from West Virginia, Virginia and North Carolina. The area of *D. carthusiana* extends south to northern Arkansas, southeastern Missouri, southern Illinois, Kentucky and northern South Carolina. Herbarium

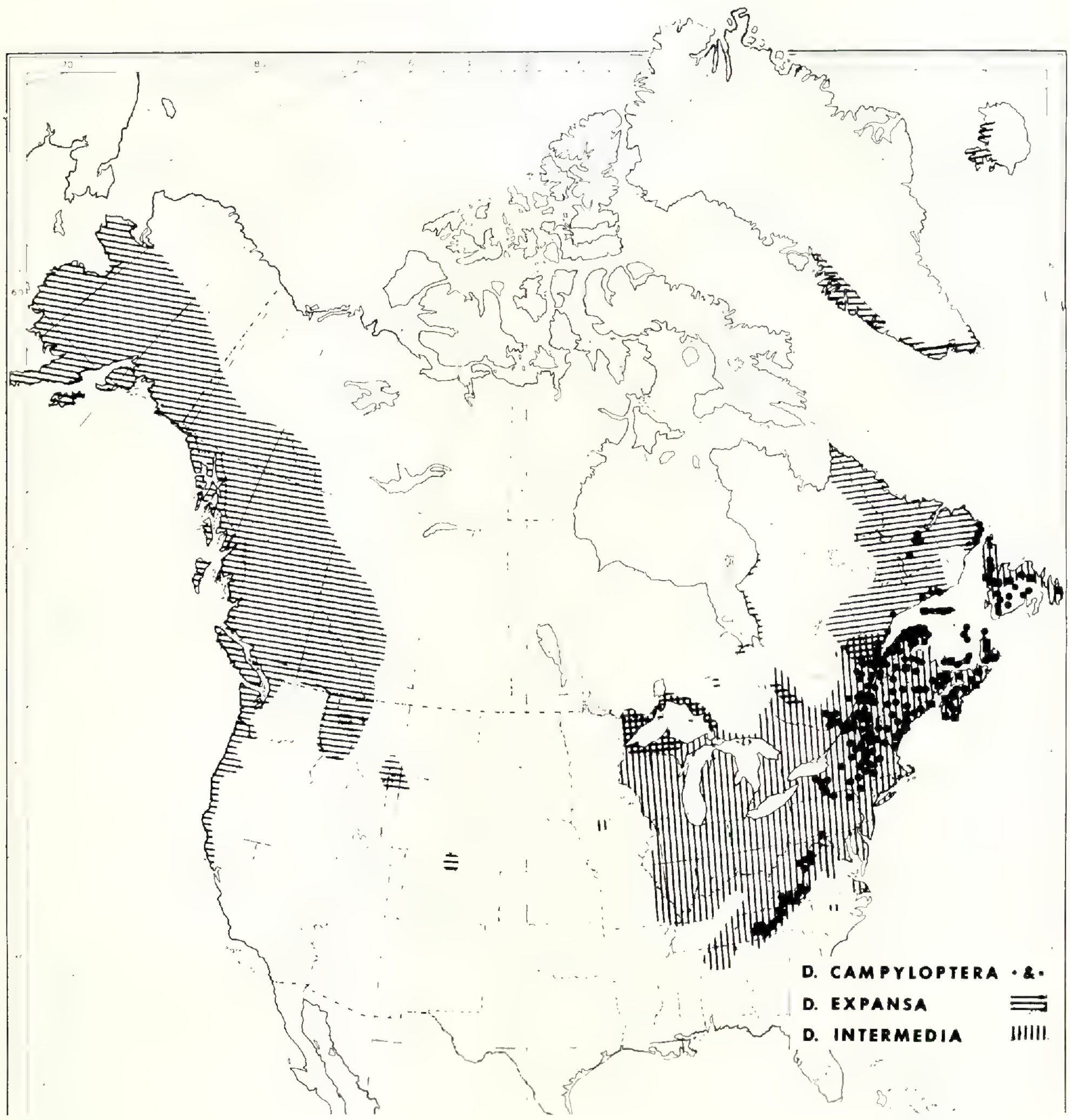

FIG. 17. *Dryopteris campyloptera* range with ranges of its parents (*D. expansa* & *D. intermedia*).

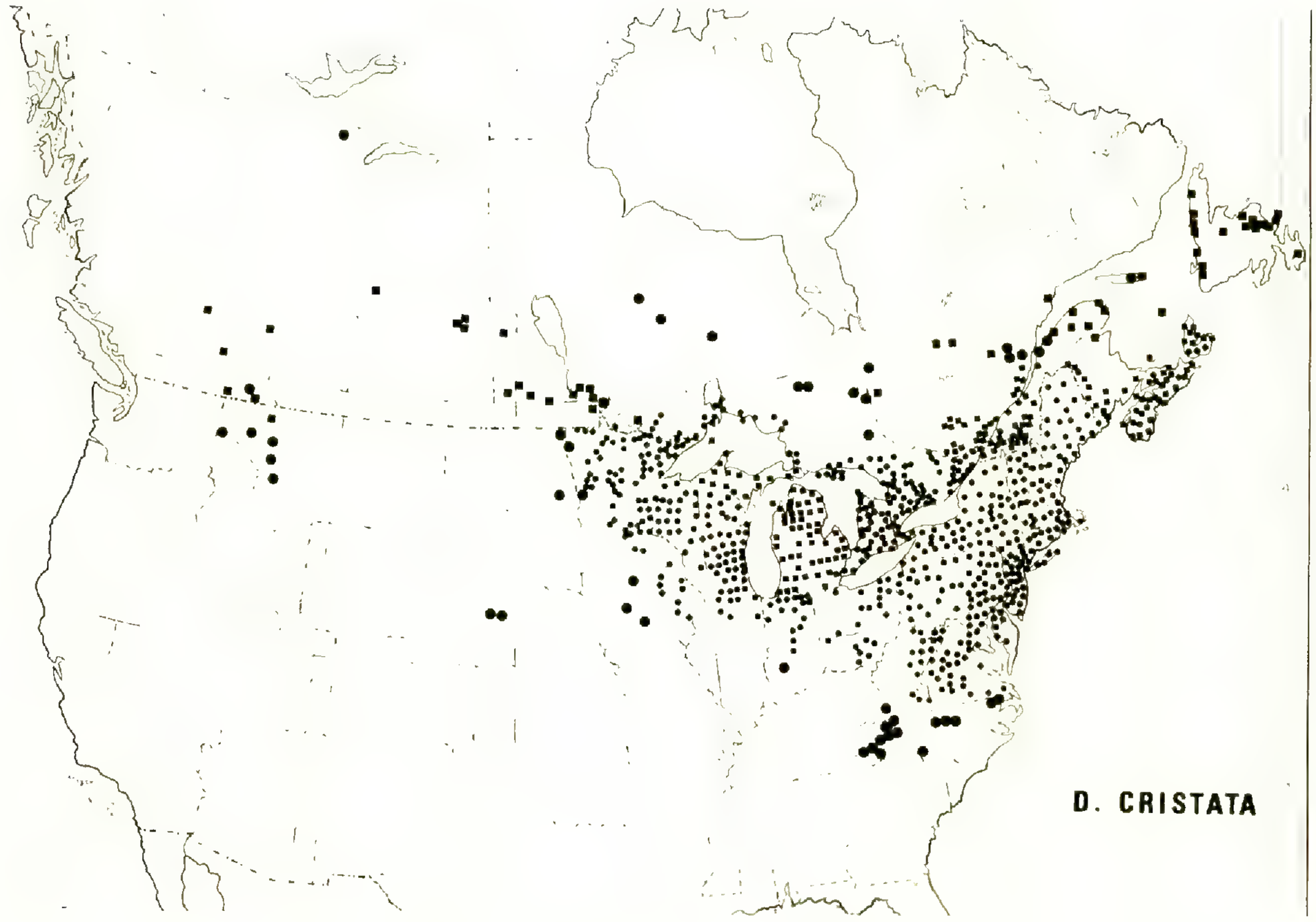

FIG. 18. *Dryopteris cristata* range in North America.

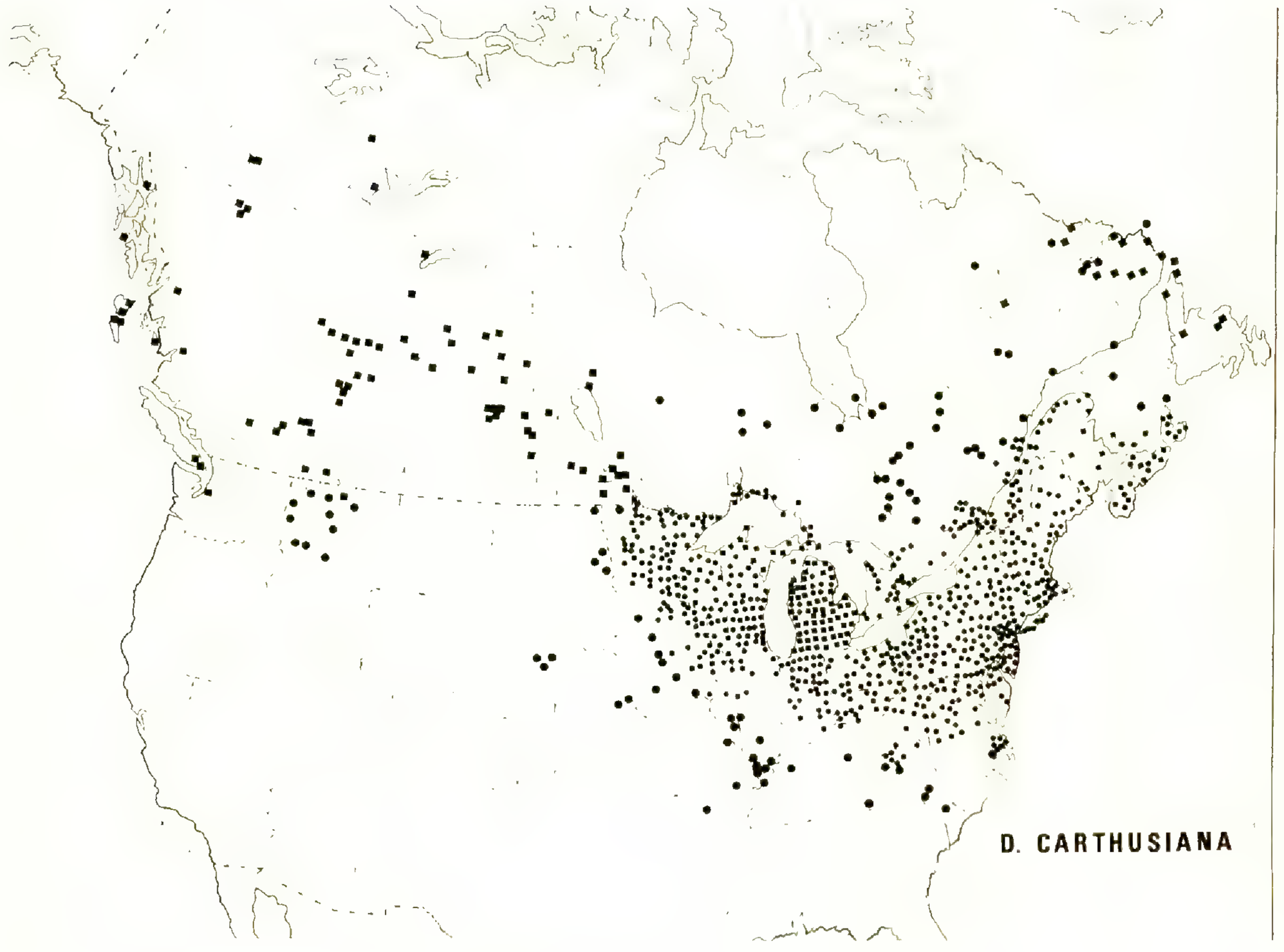

FIG. 19. *Dryopteris carthusiana* range in North America.

specimens identified as both of these species are attributed to northern Alabama, but living populations are not known to us in this area.

In eastern Canada *D. cristata* grows as far north and east as Newfoundland while *D. carthusiana* ranges farther north through Labrador and Quebec. Both species extend westward across Canada to the Rocky Mountains. West of the northern Great Lakes the range of *D. cristata* constricts into a narrow band of scattered localities through southern portions of Manitoba, Saskatchewan and Alberta to the Rocky Mountains (southeast British Columbia, southwest Alberta, northern Idaho and northwest and west central Montana). *D. cristata* also has a disjunct locality near Lake Athabaska in northern Alberta. *D. carthusiana* likewise has a band of scattered localties running through the plains provinces but they are farther north than those of *D. cristata*. The range of *D. carthusiana* also reaches farther north in western Canada and farther west to the Pacific Coast extending as far north as Juneau, Alaska and as far south as Northwest Washington. Populations are also known in northern Idaho, northwest Montana and northward through Alberta and British Columbia in the Rocky Mountains to MacKenzie. In the Old World *D. cristata* grows mainly at middle latitudes in Europe with disjunct populations in central Russia (Fig. 20). *D. carthusiana* (Fig. 21) reaches farther eastward and northward in Europe. The eastern end of its range constricts into a narrow band which extends through middle latitudes of central Russia.

DISCUSSION

We here consider some of the major geological and climatological events to which the species have been exposed during their histories. The ranges of *D. expansa* (Fig. 6) and *D. filix-mas* (Fig. 3) have in common a gap between the Rocky Mountains and the Great Lakes region (with the exception of *D. filix-mas* populations in the Black Hills). Perhaps before the Pleistocene their ranges were continuous but during the glacial maxima they became discontinuous to the south of the ice and to the east and west of the Great Plains. Following the final retreat of the ice sheet the northward migration did not re-establish continuous ranges because of the vast open grasslands. These prairie habitats evidently exclude all *Dryopteris* species. At present some of the species (*D. intermedia, D. marginalis, D. goldiana, D. ludoviciana, D. celsa, D. clintoniana, D. campyloptera*) (Figs. 8–11, 12, 14, 16) occur only to the east of the Great Plains; one (*D. arguta*) grows only to the west; some (*D. expansa, D. filix-mas*) (Figs. 6, 3) grow to the east and west, while others (*D. fragrans, D. cristata, D. carthusiana*) (Figs. 1, 18, 19) are continuous across much of North America with the central parts of their ranges however occupying only areas north of the Great Plains. These continuous populations may have been retained through the Pleistocene epoch or perhaps separated populations from the east and west converged and rejoined as the glacier retreated. The main source of North American Woodfern diversity was perhaps eastern Asia. Some taxa probably migrated across land at higher latitudes into the New World during the Tertiary or during interglacial periods of the Pleistocene.

Only two sexual taxa have been derived from tropical America. These primarly Mexican species barely extend into the southwestern United States. They are *Dryopteris patula* (Sw.) Und. var. *rossii*, a diploid of sheltered cliffs in southern Arizona (Kearny & Peebles, 1951), and *D. cinnamomea* C. Chr., found in a cave in Val Verde County, Texas (Reeves, 1978) the chromosomes of which are unreported.

Five of the 15 sexual Woodfern taxa in North America have circumboreal (circumpolar or amphioceanic) affinities while several others have Cordilleran and (or) Appalachian affinities with closely related counterparts in eastern Asia

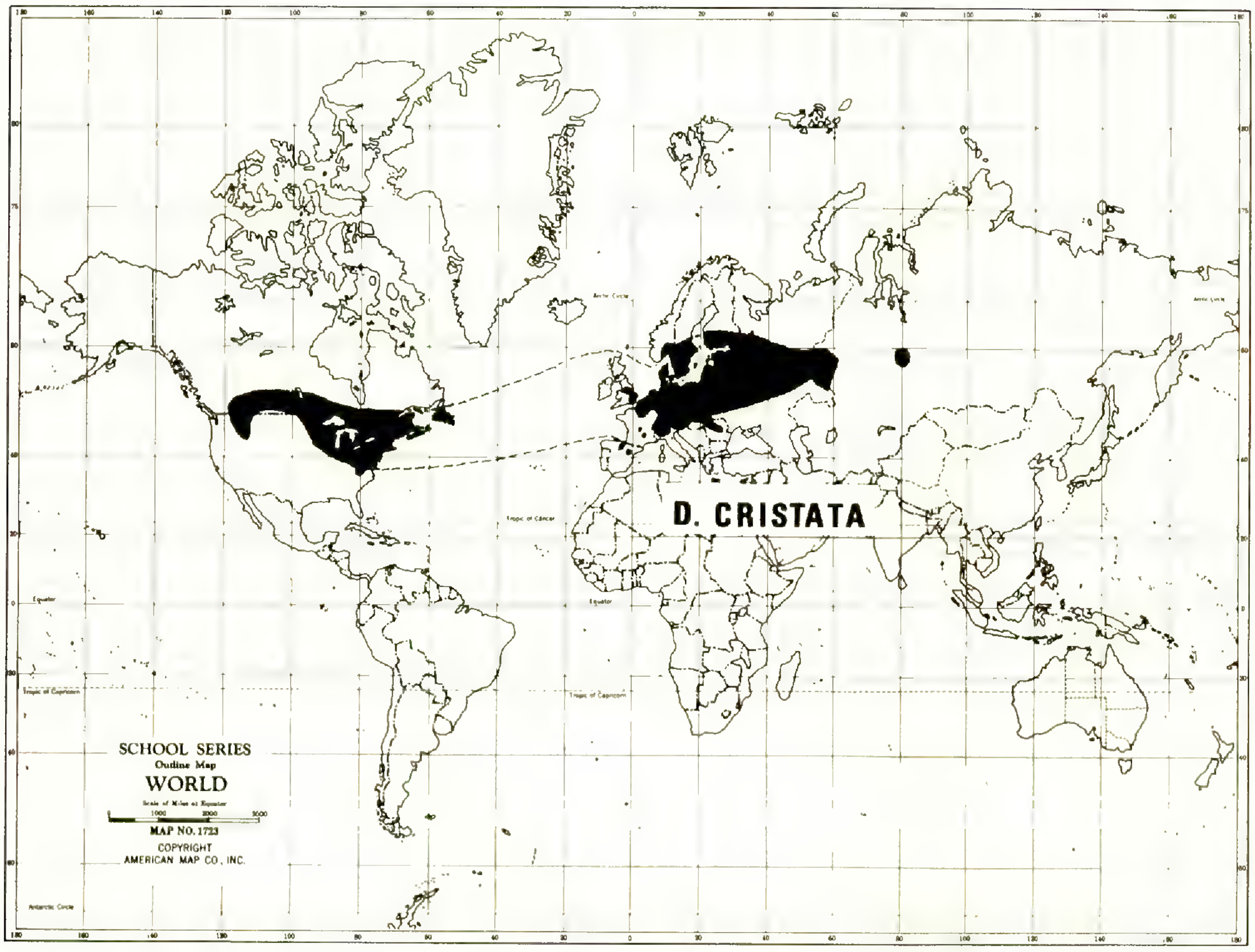

FIG. 20. *Dryopteris cristata* approximate global range.

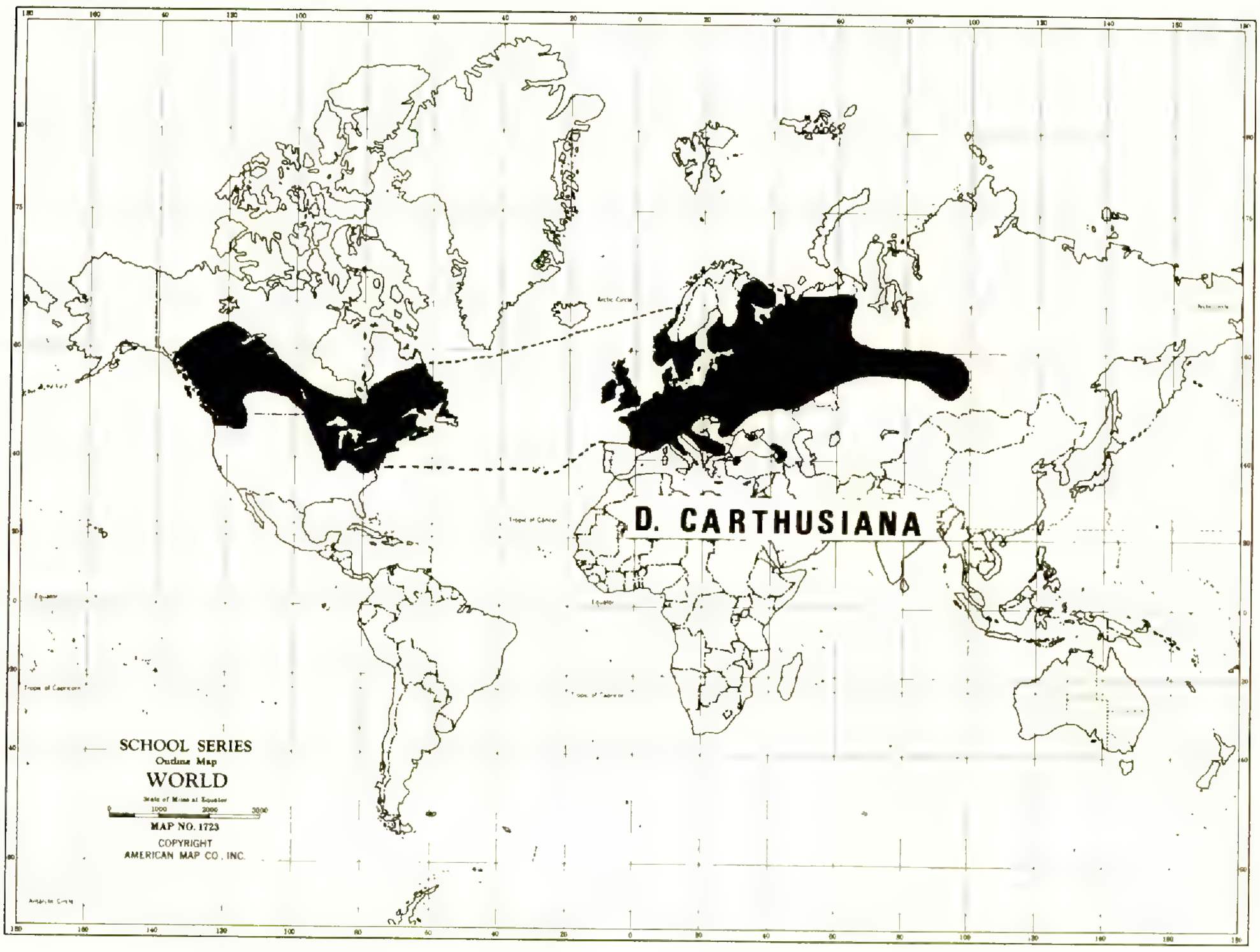

FIG. 21. *Dryopteris carthusiana* approximate global range.

and (or) in Europe. A. C. Jermy (*in litt.*, 1979) suggests that *D. arguta* may be closely related to the Old World *D. villarii (rigida)*-*D. pallida* complex of Europe and Asia.

Such vicarious affinities suggest that this western North American range may be a relic of a once widespread arctotertiary distribution. Other eastern North American Woodferns that may have Old World vicarious affinities will be discussed below. Many of these may have had ancestral arctotertiary ranges of which only isolated relicts at lower latitudes exist today. During the Pleistocene epoch fluctuating climatic and geologic conditions altered ranges in northern latitudes.

The distributions of the five North American allopolyploids will be analyzed in respect to the ranges of their respective parents. Since the present ranges of the parents of *D. celsa* (*D. goldiana*, and *D. ludoviciana*) (Figs. 12, 11, 10) do not overlap (Wagner & Wagner, 1965), it seems likely that during the advances and retreats of the ice sheet the two ranges conjoined and hybrids were formed which went through polyploidization to form the fertile allotetraploid, *D. celsa*. When the ice sheet finally retreated *D. goldiana* migrated northward separating from *D. lucoviciana*, and the newly formed *D. celsa* established a range (Fig. 12, 13) that is latitudinally and altitudinally intermediate between those of its parents (Wagner, 1971).

Dryopteris clintoniana (Fig. 14) probably resulted from the many disturbed habitats left by the glacier. These habitats allowed for its parents (*D. cristata* and *D. goldiana*) to become established in close proximity as their ranges followed the retreating ice sheet northward (Wagner, 1971). Hybrids formed which underwent polyploidization to form *D. clintoniana*. Its distribution is latitudinally intermediate between and narrower than its parents (Figs. 10, 14, 15, 18), restricted to land covered by deposits of glacial till. The southern border of its range faithfully follows the southern boundary of the ice sheet advance. The fern's localization on glacial till may be a major factor limiting the expansion of its range to the south or north.

The parents of *D. campyloptera*, *D. expansa* and *D. intermedia*, overlap in the northern Great Lakes, southwest Quebec, in the Gaspe Peninsula, Anticosti Island, north of Anticosti Island on the southern coast of eastern Quebec, and west of the Gaspe Peninsula on the northwest shore of the St. Lawrence River, and in the Saguenay River Valley. However, the primarily Appalachian distribution of *D. campyloptera* (Fig. 14) does not directly reflect these areas of overlap (Fig. 15). We suspect that several times during advances of the ice sheet the two parents mingled to a much greater extent as a result of the southward extension of their ranges. Hybrids between them went through chromosome doubling to produce *D. campyloptera* which then followed the retreating glacier northward and developed its present range, the boundaries of which are more northern than those of *D. intermedia* but much more southern than those of *D. expansa*. While *D. campyloptera* may occur in low woodlands in the north, it grows southward almost exclusively in high mountain forests. This supports findings (e.g., Beaman et al., 1962; Reese, 1961a) that suggest that some polyploids are better equipped than their diploid ancestors to inhabit extreme environments at higher altitudes.

The two circumboreal (more specifically amphioceanic) allotetraploid species, *Dryopteris cristata* and *D. carthusiana* form a natural pair. Wagner (1971) suggested that these tetraploids have a common parent ("*D. semicristata*") that possessed a hypothetical SS genome and is now presumably extinct. Among the similarities between these two ferns are leaves partially deciduous, triangular basal pinnae, and preference for moist, acidic lowland habitats. Perhaps the greatest similarity is in their ranges (Figs. 18–21), although a noticeable difference is the more northerly range of *D. carthusiana*. This is not surprising since

the extant putative parent (*D. intermedia*, Fig. 8) of the former has a greater northern distribution than that of *D. ludoviciana* (Fig. 11) the parent of the latter. Since the range of each allopolyploid and one of its parents is known, the approximate range of the hypothetical missing parent, "*D. semicristata*" can be estimated.

Stebbins (1950) stated that there is a tendency for angiosperm polyploids to be more widely distributed than their diploid ancestors. This assumption is evidently not true in several primary temperate fern polyploid complexes. Hirabayashi (1974) found that distribution of the tetraploid Japanese *Dryopteris* are narrower than those of their diploid ancestors. Of temperate North American pteridophyte complexes, twelve examples were taken from the literature (Wagner, 1965, 1966; Wagner and Wagner, 1965; Smith, 1971) and from the results presented above in the present paper. Of them, most have narrower ranges than either of their parents while the rest have a distribution similar to one parent but narrower than the other. While these patterns hold true for most allopolyploid pteridophytes that have been studied, some do have ranges larger than one or both parents. For example, the areas of *D. cristata* (Figs. 18, 20) and *D. carthusiana* (Figs. 19, 21) are both larger than the existing ranges of the presumed extant parents (Figs. 8, 11), but mainly in an east-west direction. If these allopolypoids are very old the original relationship between their range and those of their parents may have become distorted and the patterns no longer evident. Genetic divergence of old polyploids probably slows down considerably and thus acts to conserve primitive ecological and distributional features while related diploids have undergone change (Ehrendorfer, 1980). Since the known parent of each, *D. intermedia* and *D. ludoviciana*, are diploids, their ranges may have shifted more than those of the allopolyploids. Their parental diploids may even have had world-wide distributions in the past. To understand the original relationships between the ranges of allopolyploids and those of their parents, the most revealing studies may be on what we assume to be fairly recently developed allopolyploids (e.g., *D. campyloptera, D. celsa,* and *D. clintoniana*). The generalized relationship between the ranges of allopolyploid pteridophytes and those of their parents has been summarized as follows (Wagner 1969): "Of the hybrid pteridophytes . . . those which are not entirely sympatric with the parents show less east-west correlation with the parental ranges than north-south. The north-south distribution is intermediate as we might expect." No matter what size the range of an allopolyploid pteridophyte is in relation to those of its parents, latitudinal intermediacy between them can usually be anticipated. Therefore, we expect that if "*D. semicristata*" were present today it would grow approximately within 50°–80° N latitude and possibly have a circumpolar distribution.

If we assume that *Dryopteris ludoviciana* is the other parent of *D. cristata* in addition to "*D. semicristata*," then the origin of *D. cristata* must have occurred in the New World. However, a native Asian diploid fern, *D. tokyoensis* (Mak.) C. Chr., with the same chromosome number as *D. ludoviciana* (2N = 82) grows in Japan, Korea, and parts of China in only slightly higher latitudes than *D. ludoviciana* and in a similar climate. (A similar vicariant relationship exists between *D. goldiana* of eastern North America and *D. monticola* C. Chr. of Japan which are morphologically similar.) *D. ludoviciana* (Fig. 22A) and *D. tokyoensis* (Fig. 22B) are similar morphologically, but the former has fronds which are slightly more dissected and pinnae which are more dimorphic than the latter. Perhaps they have a common ancestor that had a worldwide range that through time became fragmented, and geographical separation of the populations diverged into vicarious species. Where the ancestral range overlapped with that of "*D. semicristata*" in the northwestern and north central Old World, hybrids may have formed that underwent chromosome doubling to produce *D. cristata*, which eventually developed a circumboreal distribution. When the Pleistocene con-

FIG. 22. Frond A is *Dryopteris ludoviciana.* Frond B is *Dryopteris tokyoensis.*

tinental ice sheet extended southward, all the populations of the circumpolar "D. semicristata" were presumably eradicated by the advancing ice. The present eastern Asian range of *D. tokyoensis* may be a fragment of a former broad Old World range that survived the glaciation. The ability of *D. cristata* to survive the extreme conditions produced by glaciation more successfully than its diploid parents may be explained by suggestions (e.g., Stebbins, 1950; Reese, 1958, 1961a) that polyploids are better equipped than their diploid ancestors to adapt to extreme conditions since they have more alleles and therefore greater genetic flexibility. Hence the origin of *D. cristata* may have been in either the Old or the New World or possibly in both hemispheres.

Assuming that *Dryopteris intermedia* is the other parent of *D. carthusiana* in addition to "*D. semicristata,*" the origin of *D. carthusiana* may also have been in the New World. However, the Old World species, *D. madierensis* Alston and *D. azorica* (Christ) Alston, apparently possesses the same basic genome as the *D. intermedia* (Gibby, 1977; Gibby and Walker, 1977) and the three comprise a species aggregate. These findings were determined by chemical (Widén & Britton, 1969; Widén et al., 1970; Widén, Britton et al., 1975; Widén, Lounasmaa et al., 1975), cytological (Gibby & Walker, 1977) and morphological (Walker, 1961) comparisons. One difference that exists between them is that the Old World representatives do not possess the epidermal glands so characteristic of the New World *D. intermedia.* This lack of glands is important since *D. carthusiana* is glabrous or nearly so. If the glandular New World *D. intermedia* were a parent of *D. carthusiana* one would expect to find more glands on *D. carthusiana* since they are present on other North American Woodfern hybrids involving *D. intermedia.* Since *D. carthusiana* is glabrous or nearly so we suspect the existing glandular New World *D. intermedia* is not a likely immediate parent, although a glabrous New World ancestor may have been a parent of *D. carthusiana.* Presently there exist nearly glabrous populations of *D. intermedia* in the southern part of its range in the Appalachian mountains of North Carolina (Wagner, unpublished).

These "glabrous" populations are probably primitive judging from outgroup comparison with its relatives and indicate that the ancestor of the glandular *D. intermedia* was glabrous. Under these circumstances *D. carthusiana* could have originated in the New World. An Old World origin of *D. cathusiana* is, however, equally possible, even though presently *D. madierensis* is only known on the continental island, Madeira Island (450 miles from Morocco) while *D. azorica* is only known on the oceanic islands, the Azores (900 miles from Portugal). Most taxa on island floras are the same as, or related to, widely distributed continental species. The dominance of widely distributed species in island fern floras clearly reflects an ability to migrate from continents. Their proportion on islands are much higher than their proportions in source areas (Tryon, 1970). Page (1973) concluded that the Canary Island (50 miles from Cape Yubi, Africa) fern flora is largely made up of ancient species that existed in Tertiary Europe, and have survived, little changed, as relics in the island mountains. Studies on Madeira Island (I. Manton, J. D. Lovis and G. Vida, unpublished; I. Manton et al., unpublished; as cited in Lovis, 1977) have also yielded evidence that these islands may have provided refugia for forms that are no longer capable of surviving elsewhere. Accordingly the insular *D. azorica* and *D. madierensis* may actually be remnants of an ancestral range which extended through northern Africa into western and central Europe in mid-Tertiary times. Where the ancestor overlapped that of "*D. semicristata*," hybrids formed that doubled to produce *D. carthusiana* which eventually developed its circumboreal distribution. Gibby (1977) suggested that *D. madierensis* or *D. azorica* may have occurred together with *D. expansa* in the past in Europe to give rise to the allotetraploid *D. dilatata* (s. str.), which has a similar genome, and may be conspecific with the North American *D. campyloptera*. When the Pleistocene ice sheet extended southward, the entire continental range(s) of *D. madierensis* and *D. azorica* or their ancestor may have been destroyed along with that of "*D. semicristata*." These island populations survived the Pleistocene glaciation because of a buffered island habitat. The continental range of *D. carthusiana* was able to survive glaciation for the same reason mentioned above for *D. cristata*. Hence, the origin of *D. carthusiana* may also have been either in the Old World or the New World or possibly in both hemispheres independently.

In the modern arctic climate, habitat instability is still an outstanding feature, and it is likely that new polyploid races are being produced where opportunities for hybridization and successful establishment of new genotypes obtain (Johnson, Packer & Reese, 1965).

The frequency of polyploids in areas that were altered by climatic conditions of the Pleistocene epoch suggests that these environments were outside the tolerance limits of many of the existing diploid species and that they were invaded by older polyploids (e.g., *D. cristata* and *D. carthusiana*) as well as by the proliferation of new variable hybrid polyploids (e.g., *D. campyloptera, D. celsa* and *D. clintoniana*.)

SUMMARY

The 15 sexual taxa of Woodferns (*Dryopteris*) living in North America north of Mexico, display a diverse array of geographical ranges that correlate with topography, climate, past glacial activity, habitat availability. The ranges bear upon possible phylogenetic origins. Two diploids, *D. fragrans* and *D. expansa* and the tetraploid, *D. filax-mas* all have circumboreal distributions. The western *D. arguta* extends mainly through Pacific coastal ranges while *D. cinnamonea* and *D. patula* var. *rossii* reach their northern limits in southern United States. Four diploid species (*D. goldiana, D. intermedia, D. marginalis* and *D. ludoviciana*) grow exclusively in eastern North America. All of these occur from Canada south

through the Appalachians to the upper fringes of the southeastern United States coastal plains except *D. ludoviciana,* which is restricted wholly to the southeastern United States coastal plain. The other Woodferns that grow exclusively in eastern North America are fertile allopolyploids: *D. campyloptera,* mainly of northern and middle latitudes in the mountains; *D. clintoniana,* of middle latitudes; and *D. celsa,* of middle and southern latitudes. Pleistocene glaciation probaby influenced the origins of these allopolyploids by forcing co-habitation of their respective parents in response to advancement and retreat of the ice sheet. The final two North American Woodfern species (*D. cristata* and *D. carthusiana*) are both circumboreal allopolyploids. It has been suggested that they may have a common parent (SS genome) now presumably extinct. Strong similarities between the ranges of these two allotetraploids support this suggestion. Their origin may have been either in the Old World or the New World or possibly in both hemispheres.

ACKNOWLEDGMENTS

We thank Donald M. Britton, Michael G. Price, and A. A. Reznicek for reviewing the final manuscript. We also are grateful for help in various ways to P. Adams, D. J. Bay, J. M. Beitel, W. S. Benninghoff, J. G. Bruce, R. B. Cranfill, J. D. Freeman, C. H. Haufler, R. Haynes, M. J. Huft, A. C. Jermy, D. M. Johnson, D. B. Lellinger, R. Kral, M. R. Mesler, J. T. Mickel, R. S. Mitchell, R. H. Mohlenbrock, J. D. Montgomery, G. B. Ownbey, J. H. Peck, T. Reeves, J. Senko, J. W. Short, A. R. Smith, W. C. Taylor, J. W. Thieret, R. M. Tryon, G. R. Upchurch, E. G. Voss, F. S. Wagner, K. S. Walter, and J. R. Wells. We also acknowledge the curators of several herbaria for supplying herbarium specimens for study. These herbaria are BLH, CAN, CI, DAO, GH, IND, KY, MICH, MIL, MIN, MPPD, MT, MTMG, NYS, TKB, UC, UNA, UWL, WIS, and WTU.

This research was supported by NSF grant DEB-03550 A01.

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THE ITINERARY OF MARY STRONG CLEMENS IN QUEENSLAND, AUSTRALIA

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The names of Joseph and Mary Strong Clemens will long remain legend in the Philippines, in Borneo, and in New Guinea. Their botanical specimens housed in herbaria throughout the world will stand as a testimony of their many years of collecting in those areas and as a valued contribution to the science of botany. Forced by the Japanese invasion to flee from New Guinea (where she had remained following the death of her husband in 1936), Mrs. Clemens arrived in Brisbane, Australia, on 31 December 1941 aboard a special train for refugees, and there she made her home. At an age when most of us would be content to take life a bit easier, she commenced field work in Queensland. Her journal, whose daily entries commence with a notation about the weather and a quotation from the Scriptures, shows her celebrating her 71st birthday (3 January 1944) by a collecting trip to the summit of Mount Mistake near Brisbane. During the war years most of her collecting was confined to short trips in the vicinity of Brisbane. After the war, and until early in 1950, she made at least one or two longer collecting trips annually. Mrs. Clemens died in Brisbane on April 13, 1968, at the age of 95. Her collections have served as the basis for a number of the new species included by C. T. White in his "Contributions to the Flora of Queensland." These have appeared in various numbers of the Proceedings of the Royal Society of Queensland.

Sets of most of the collections made by Mrs. Clemens during the period from 1943 through 1950 were sent to Professor H. H. Bartlett, Director of the Botanical Garden of the University of Michigan, Ann Arbor, Michigan, U.S.A., who undertook the distribution and sale of duplicates in Mrs. Clemens' behalf. Professor Bartlett's extensive correspondence with Mrs. Clemens is on file at the University of Michigan Herbarium. It was in connection with the distribution of these duplicates that preparation of an itinerary of Mrs. Clemens' Queensland field work seemed advisable in order to clarify some inconsistencies that appeared on the labels. The major part of the itinerary was compiled from the collections during 1957–1958 while the author was in residence at the University of Michigan processing the herbarium collections amassed by H. H. Bartlett. Later, through the courtesy of Dr. S. L. Everist of the Brisbane Botanic Garden, Mrs. Clemens' journals were made available to the writer. She consulted them again in Brisbane in 1976. The cooperation of Dr. Rogers McVaugh and of Mrs. Robert Dieterle, both of the Herbarium of the University of Michigan, is much appreciated.

The collections which Mrs. Clemens made during the period from February 1943 through October 1944 (in part) were assigned consecutive field numbers in continuation of the series begun by Mr. and Mrs. Clemens. Assignment of these field numbers was made at the University of Michigan, rather than in Queensland by Mrs. Clemens. These numbers, assigned under the direction of Professor Bartlett, ran from 41,964 to 44,767. Consequently, duplicates of type specimens may bear a collection number whereas the holotype housed in the

Brisbane Botanic Garden does not bear a number. Subsequent collections, through January 1950, were not assigned field numbers. Including duplicates, approximately 18,380 sheets of Mrs. Clemens' Queensland collection were processed at the Herbarium of the University of Michigan. In addition to the set at the University of Michigan, the following institutions received sets of these duplicates: Botanic Museum and Herbarium, Brisbane; British Museum; Chicago Natural History Museum; Conservatoire and Jardin Botaniques, Genève; Gray Herbarium of Harvard; Naturhistoriska Riksmuseet, Stockholm; New York Botanical Garden; Rijksherbarium, Leiden; Royal Botanic Gardens, Kew; State University of Iowa; United States National Herbarium; University of California Herbarium, Berkeley.

In the following itinerary, dates for specimens collected in the immediate vicinity of Brisbane have been omitted. When Mrs. Clemens does not use the term "station" in the usual Australian sense of "homestead" or huge sheep ranch, she specifies that the locality is at a railroad station. Figures 1–3 illustrate Mrs. Clemens' collecting localities.

An illuminating account of Mrs. Clemens, as a person and a botanical collector, written by R. F. Langdon, is included in *People and Plants in Australia* (edited by D. J. and S. G. M. Carr, published by Academic Press, Sydney, New York, London, et al., 1981). It injects life into the itinerary!

1942

February to December: some collections in the vicinity of Brisbane.

1943

January: some collections in the vicinity of Brisbane. February 9, 24, 29, Mt. Coot-tha. March 2, 4, Cooper's Plains [SW of Sunnybank, S of Brisbane]; 9, near Clermont; 11, Mt. Gravatt [S of Brisbane]; 22, Ashgrove; 29, Stafford. April 5, Ferny Grove; 19, Thornside Station, Birkdale; 26, Lawnton, Petrie. May 3, Kalinga, Clayfield; 11, Lockyer Valley; 18, Kenmore; 22, Lone Pine, Kenmore; 28, Ngun-gun, Glasshouse Mountain, near summit. June 7, near Mt. Gravatt; 11, Landsborough; 12, Beerwah; 22, Sunnybank; 29, Pine Mountain. July 3, Elimbah [N of Brisbane]; 6, Mt. Elimbah, summit saddleback, Elimbah; 15, Mt. Coot-tha, Taylor Range; 20, Nugee, Virginia, Banyo; 26–27, Landsborough, Caloundra, Mooloolah. August 5, Sunnybank; 6, Sherwood; 10, Sherwood Arboretum; 16–17, Cooper's Plains; 23, Mt. Gravatt; 30, Mt. Gravatt, Sunnybank. September 7–9, Tugun; 20, Chermside; 21–22, Glasshouse Mountain; 22, Caloundra; 30, Chermside, Woolscour. October 5, Caloundra; 12, Ferny Grove, Sanford Range; 19, Brisbane to Springbrook via Mudgeeraba; 20–28, Springbrook National Park; 29, returned to Brisbane via Mudgeeraba. November 10, from Brisbane to Stanthorpe; 11–12, Stanthorpe; 13, Stanthorpe to Liston (N.S.W.); 14–18, Liston; 19, Liston to Stanthorpe to Warwick to Toowoomba; 20, Toowoomba to Ipswich to Brisbane; 26–27, Springbrook. December 21, Brisbane to Imbil, Lutton's Saw-mill; 22–30, Imbil; 30, Imbil, Gympie; 31, return to Brisbane.

1944

January 3, Mt. Mistake, summit; 18, Rosewood, Thagoona railroad station, Redwood; 25, Brisbane to Laidley, Currumbin; 25–31, Laidley (Laidley hills, Forest Hill, Grandchester). February 1–4, Mt. Mistake; 4, Mt. Mistake, from summit to Crosby's to Laidley; 5, Laidley to Brisbane; 17, Brisbane to Crows Nest; 18, Crows Nest, Peechey; 19–24, Crows Nest; 25, Crows Nest via

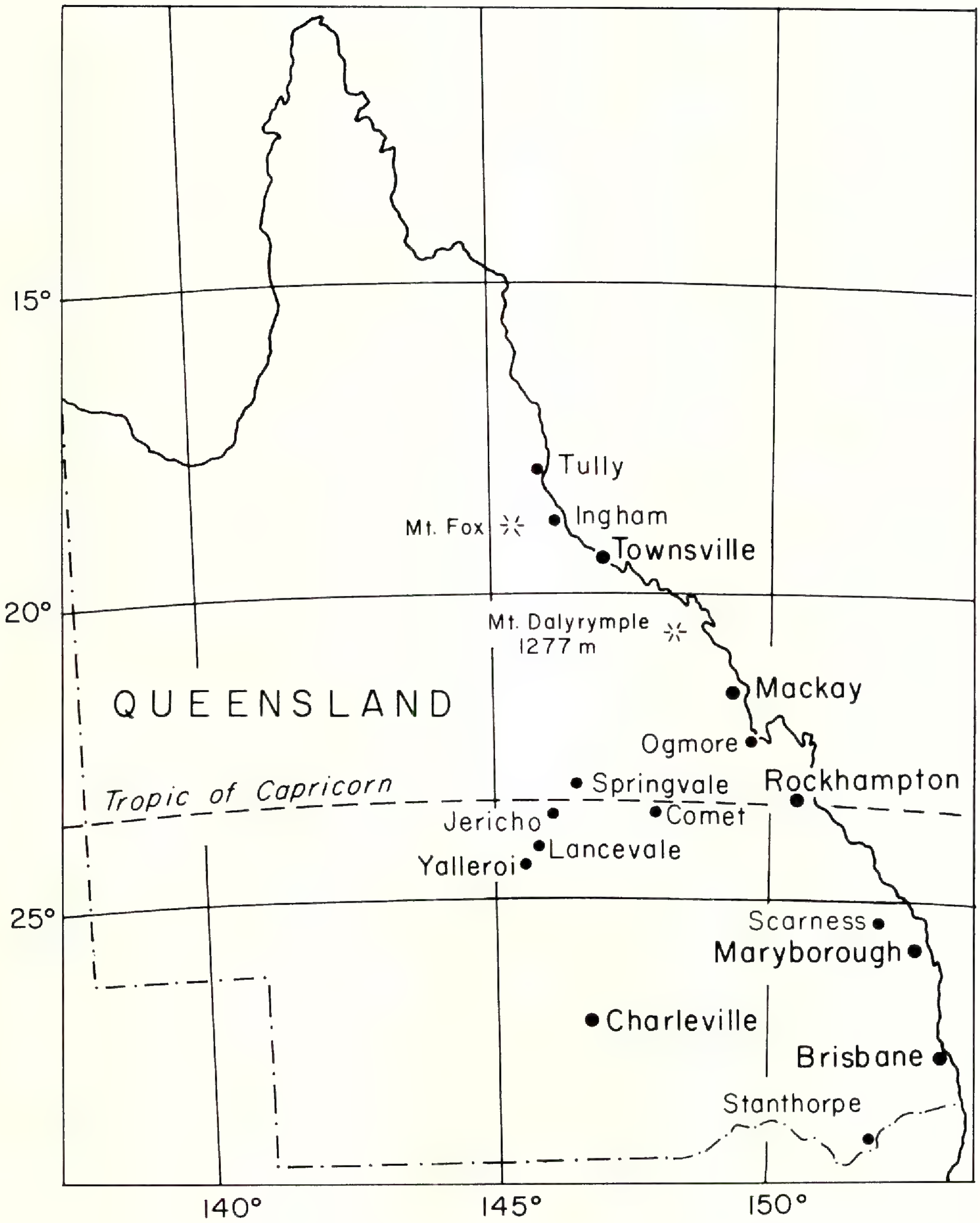

FIG. 1. Principal collecting localities on Mrs. Clemens' extended trips in Queensland.

Toowoomba to Brisbane. March 15, Brisbane to Kingaroy, "152 miles via bus"; 16, Kingaroy; 17, Kingaroy to logging camp in Bunya Mountains; 18–24, Bunya Mountains, sawmill near summit; 25, Bunya Mountains to Toowoomba via Dolby; 26, return to Brisbane. April 18, Brisbane to Bribie Island; 20–30, Bribie Island. May 1, Bribie Island; 2, Bribie Island to Brisbane; 23, Brisbane to Stradbroke Island; 26, Stradbroke Island: pumping station to Amity Camp from Dunwich; 27, Amity to One Mile, Dunwich; 28–31, Dunwich. June 1–6, Stradbroke Island; 6, Dunwich to Brisbane. July: Brisbane. August 1, Brisbane to Yarraman; 18, Yarraman to Brisbane. September [no definite dates]: Sanford, Sunnybank, Tambourine Mountain. October 5, Brisbane to Wallangarra; 6–19,

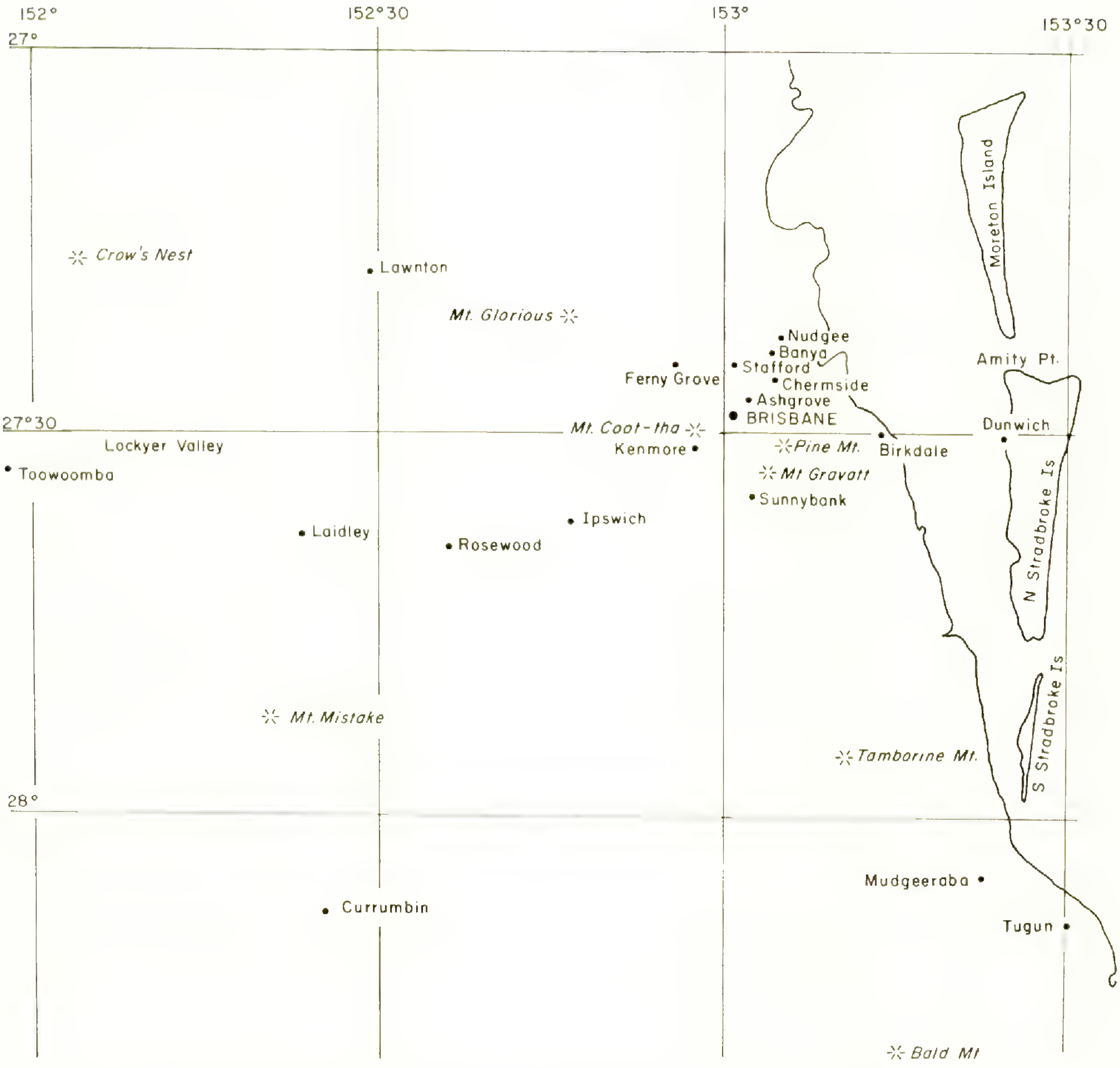

FIG. 2. Principal collecting localities on Mrs. Clemens' shorter trips (west and south of Brisbane).

Wallangarra (Ballandean, Stanthorpe, Goebel's place, Barber's ranch, Bald Mountain, Granite National Park [Girraween National Park] near Wyberba); 20, Ballandean to Warwich; 21, Warwich to Brisbane. November 7, Brisbane to Wallangarra; 8–19, Granite National Park [Girraween National Park], Wyberba (Mt. Norman, Bald Mountain, Wallangarra, Eukey, Goebel's, Bedford's, Ballandean; 20, Eukey to Ballandean railroad station; 21, Ballandean to Brisbane. December 22, Brisbane to Mt. Glorious; 23–31, Mt. Glorious.

1945

January 1–31, Mt. Glorious. February 1, Mt. Glorious; 2, Mt. Glorious to Brisbane. March 22, Brisbane to Coolum Beach, Yandina; 23, Coolum Beach to Mt. Coolum; 24–31, Mt. Coolum. April 1–3, Mt. Coolum; 3, Mt. Coolum to Coolum Beach; 4–5, Coolum Beach; 6, Coolum Beach to Brisbane. May: some collections around Brisbane. June 1, Brisbane to Gundiah; 2, Gundiah via Tiaro to Bauple; 3–22, Mrs. Clemens' notebook entries for these dates are "Bauple, MacKellar's cabin." The entries obtained from labels are as follows: June 6, Bauple, open bush; 7, 8, 9, Bauple; 10, Bauple, bush margin, Bauple mountains; 11, 14, Bauple mountains; 15, Bauple, margin of pond; 16, 17, Bauple; 18, Mount Bauple, near Bauple, Tenina Creek; 19–21, Mount Bauple; 23, Bauple to

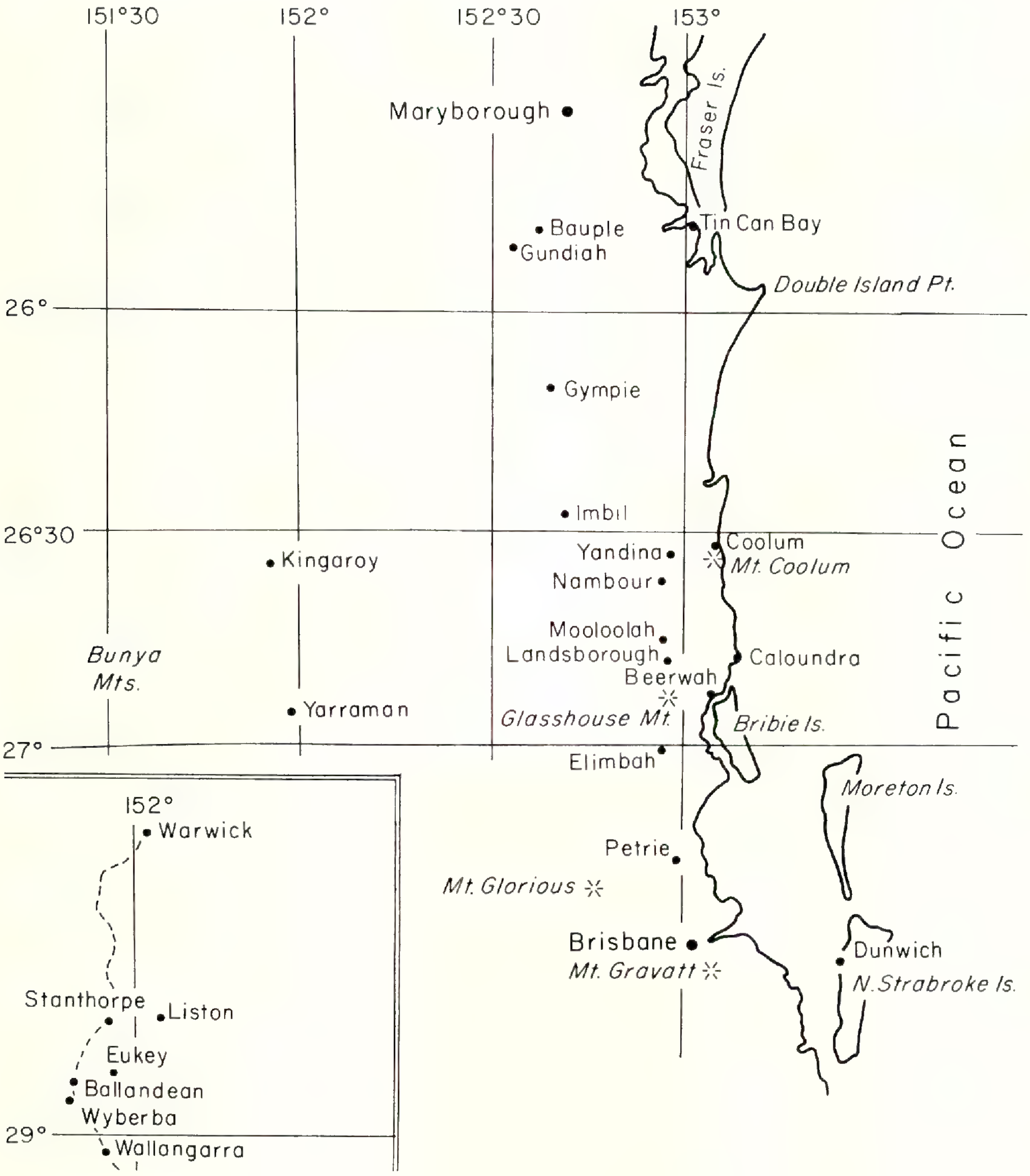

FIG. 3. Principal collecting localities north and northwest of Brisbane. Insert extends southward into New South Wales.

Brisbane. July and August: some collection around Brisbane. September 18, Brisbane to Toowoomba and westward; 19–30, Charleville. October: Charleville. November 1–28, Charleville (Thompson's ranch, Barrien's farm, Phillott's paddock, Dr. Fox's house); 29, Charleville towards Brisbane; 30, "from the desert to Brisbane." December: some collections around Brisbane.

1946

January: some collections around Brisbane. February: some collections around Brisbane; 28, on "train from Brisbane via Rockhampton for Jericho desert." March 1, on train from Brisbane via Rockhampton for Jericho; 2, on train from Rockhampton via Alpha to Jericho; 3–30, Jericho. April 1, Jericho to Ightham Station; 2, Springvale; 3–5, Ightham (14 miles from Jericho); Ightham to

Jericho; 7–9, Jericho; 10, Jericho to Yalleroi; 11–17, Yalleroi; 18, Yalleroi to Lancevale (13 miles from Yalleroi); 19, Lancevale; 20, Lancevale to Jericho; 21–28, Jericho; 29, Jericho toward Blackall, 20 miles from Jericho; 30, Jericho. May 1–6, Jericho; 7–9, Springvale (Ightham Station); 10–12, Jericho; 13, Jericho to Comet; 14, Comet, Emerald, to Bluff; 15, Bluff to Rockhampton; 16, "travel all night, reach Brisbane at 6 a.m." June, July, August: some collections around Brisbane. September 4, Brisbane to Gympie; 5, Gympie to Tin Can Bay; 6–27, Tin Can Bay; 28–29, Tin Can Bay and across Bay to camp; 30, "camp across Bay" on sandy beach to Double Island Point lighthouse. October 1, Tin Can Bay, Double Island Point; 2–4, Double Island Point (near lighthouse); 5–13, Tin Can Bay; 13–18, Double Island Point; 19–21, Tin Can Bay; 22, Tin Can Bay to Brisbane. November and December: Brisbane.

1947

January: Brisbane. February 28, Brisbane to Tambourine Mountain. March: Tambourine Mountain (1, Tambourine Mountain, ca. 2,000 ft. elevation; 2, Rosser's P.O., near St. Bernard Hotel; 3, Rosser's P.O. to Mrs. Holloway's; 4–13, Frank Holloway's truck farm; 14, Tambourine Mountain, ca. 1,800 ft. elevation; 15–31, Frank Holloway's truck farm). April 2, Tambourine Mountain to Brisbane. May: Brisbane. June 16, from Brisbane en route to Mackay; 18–26, Mackay; 27, Mackay to Netherdale; 28–29, Netherdale; 30, Netherdale to Eungella, Dalyrymple Heights. June 30 to November 28: Dalyrymple Heights (Bee Creek, Broken River, Crediton Parish, Eungella Range, Eungella National Park); November 29, Dalyrymple Heights; 30, Ogmore. December 1, Ogmore; 2, Rockhampton to Brisbane.

1948

January through August: Brisbane. September 1, Brisbane (via Maryborough) to Scarness; 5, Scarness; 6, Scarness to Maryborough. September 6 to November 17, Maryborough; 18, Maryborough to Brisbane. December: Brisbane.

1949

January through August: Brisbane. September 1, Brisbane via train en route to Ingham; 2, en route to Ingham; 3, past Mackay to Ingham; 4–7, Ingham parsonage; 8, Kelly Ranch, "Kelly Station," Mount Fox. September 9 to December 13: Mount Fox (Kelly Station, near Dickson's, Michael Creek, near Moreton sawmill). December 14, from Mount Fox via Ingham to Tully; 15–31, Tully and vicinity (Mission Beach, Mitchell Park gully, Fenby estate, margin of Jarrah River).

1950

January 1–16, Tully and vicinity; (3rd, "my birthday, 77th"); 21, Mackay en route to Brisbane.

ERRORS WHICH ARE KNOWN TO OCCUR ON LABELS ACCOMPANYING MARY S. CLEMENS' QUEENSLAND SPECIMENS

Brisbane, 9 November 1945 (*Chloris virgata*). Mrs. Clemens was in Charleville in November 1945.

Comet, 14 May 1945, should read 14 May 1946. Mrs. Clemens' notebook gives Brisbane for May 1945.

Ightham Station, 2 April 1947, should read 2 April 1946.
Jericho, 13 November 1944. Mrs. Clemens was at Wallangarra on this date. She collected in Jericho in March, April and May 1946. Her printed labels for "Jericho and Vicinity" read "March–April 1946." She left Jericho on 13 May and had collected in the area at least until 9 May.
Jericho, 29 October 1946. Mrs. Clemens was at Tin Can Bay on this date and at Jericho in March, April and May 1946.
Lancevale, 8 April 1946, should probably read 18–19 April.
Maryborough, 23 & 30 February 1948; 6 January 1949. Mrs. Clemens' notebook gives Brisbane for these dates. (She collected in Maryborough during September, October and November 1948.)
Mount Coolum, 2 March 1945 (*Exocarpus*). Mrs. Clemens' notebook gives Brisbane for this date. She was at Mt. Coolum from 23 March to 3 April 1945. Many labels read "March 1945."
Mount Fox, 28 December 1949 should read 28 November 1949.
Mount Mistake, 27 June 1944 (and other June 1944 dates): Mrs. Clemens' notebook gives Brisbane for June. She was at Mount Mistake 1–4 February 1944.
Mudgeebara, 29 October 1943, should read Mudgeeraba, 29 October 1943.
Springbrook National Park, 20–25 September 1943, should read 20–28 October 1943.
Springbrook, 15 October 1943. Mrs. Clemens was in Brisbane on this date and did not go to Springbrook until 19 October.
Sunnybank, 5 August 1945 (*Cladium*), should read 5 August 1943.
Tully and Vicinity, 29–30 November 1949 should read 29–30 December 1949. The printed labels for Tully and Vicinity read, "January 1950." Mrs. Clemens arrived in Tully on 15 December 1949 and collected there the balance of the month, as well as during January 1950.

Contr. Univ. Mich. Herb. 15:171–175. 1982.

THE GENUS *MIRANDEA* (ACANTHACEAE)

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This paper is part of a series of monographs, revisions, and synopses of predominantly Mexican Acanthaceae. The ultimate goal of the series is to provide a systematic treatment of the family for Mexico and surrounding regions. Other genera already treated are *Carlowrightia* (Daniel, 1980; Daniel, 1983a) and *Holographis* (Daniel, 1983b).

The genus *Mirandea* comprises two species of shrubs which occur in the arid regions of northeastern Mexico. The genus was described by Rzedowski in 1959 based on *M. grisea* from San Luis Potosí. Subsequently, Daniel (1979) described a second species from Nuevo León. Despite their occurrence in accessible regions close to the United States, the species of *Mirandea* were not described until relatively recently and both are poorly known in herbaria. The reasons for this appear to be twofold. First, little work has been done on the taxonomy of Mexican Acanthaceae since Standley's (1926) treatment of the woody species in *Trees and Shrubs of Mexico*. In that work, Standley apparently referred a specimen of *M. huastecensis* to *Carlowrightia parvifolia* Brandegee. Secondly, although the species are capable of forming extensive populations, both are restricted in distribution. Continued botanical exploration in northeastern Mexico will undoubtedly result in the discovery of additional local species of Acanthaceae.

Using the classificatory scheme of Bremekamp (1965), *Mirandea* would be included within the tribe Justicieae subtribe Odontoneminae where its closest relatives appear to be *Carlowrightia* A. Gray and *Anisacanthus* Nees. In addition to a number of common vegetative and floral characters, these genera all have the same basic pollen type and chromosome number. The pollen of each genus is prolate and tricolporate with six pseudocolpi. A chromosome number of 2n = 36 has been reported for four species of *Carlowrightia* (Reveal and Spellenberg, 1976; Daniel, 1980) and two species of *Anisacanthus* (Grant, 1955). Herewith is reported the first count for *Mirandea* of n = 18 in *M. grisea* (*Daniel 331*). These three genera can be distinguished by the following key:

1. Stamens appressed to the upper lip of the corolla, the filaments twisted, the anthers opening toward the lower lip; style recurved near the apex. *Mirandea.*
1. Stamens not appressed to the upper lip of the corolla, the filaments not twisted, the anthers opening toward the upper lip; style straight near the apex.
   2. Stout shrubs to 3 m high; corolla bright red or orange, 30–60 mm long. *Anisacanthus.*
   2. Suffrutescent herbs or weak shrubs, usually less than 1 m high; corolla white, cream or blue, 6–20 (–27) mm long. *Carlowrightia.*

Mirandea Rzedowski, Ciencia (México) 19: 80. 1959.

Erect, much-branched shrubs to 1 m tall. Older stems brown, usually fissured, pubescent or glabrate. Younger stems greenish, multi-striate, pubescent with eglandular trichomes. Leaves opposite, subsessile or petiolate, the laminas

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to 20 mm long and 7 mm wide, acropetally reduced to flower-bearing bracts. Inflorescence spicate or racemose or consisting of panicles of spikes or racemes. Flowers opposite or alternate along the inflorescence axes, sessile or short-pedicellate, subtended by 2 bractlets, the flowers and bractlets sessile or pedunculate in the axil of a bract. Calyx deeply 5–lobed, the lobes subulate, often glandular pubescent. Corolla bluish or rose-colored, bilabiate, the tube ampliate above, the upper lip erect, bifid, the lower lip 3–lobed, the lobes spreading. Stamens 2, appressed to the upper lip of the corolla, the filaments twisted just below the anthers, the anthers dorsifixed, bithecous, the thecae homomorphic, parallel, basally rounded, subequally inserted on the filament. Pollen prolate, tricolporate, each colpus flanked by pseudocolpi. Style pubescent, recurved just below the stigma. Stigma bilobed. Capsule stipitate, the head ovoid, pubescent. Seeds 2 (–4) per capsule, subcirculate, laterally flattened, obliquely notched at base, the testa granulate.

Type species: *M. grisea* Rzedowski.

Distribution: Endemic to the eastern and southern periphery of the Chihuahuan Desert Region of northeastern Mexico (Fig. 1).

KEY TO THE SPECIES OF *MIRANDEA*

Leaves subsessile, 3–10 mm long, the magins flat, ciliate; inflorescence racemose, the flowers pedunculate, not opposite, usually borne on only one side of the axis; bracts narrowly ovate to narrowly elliptic, 2–4 mm long, eglandular; corolla rose-purple. *M. huastecensis.*

Leaves petiolate, 7–20 mm long, the margins revolute, not ciliate; inflorescence spicate, the flowers sessile, opposite; bracts lanceolate to subulate, 4.5–6.0 mm long, occasionally glandular; corolla blue-purple. *M. grisea.*

Mirandea huastecensis T. F. Daniel, Systematic Botany 3: 428. 1979. Type: Mexico: Nuevo León: Huasteca Canyon, 1.4 mi. S of the Centro Recreativo La Huasteca, ca. Lat. 25°38′N, Long. 100°27′W, *Daniel 252* (MICH!, holotype; ASU!, CAS!, CHAPA!, DUKE!, ENCB!, F!, GH!, INIF!, K!, MEXU!, MO!, NY!, TEX!, UC!, US!, WTU!, isotypes).

Younger stems pubescent with an overstory of stiff, erect to retrorse trichomes 0.3–07 (–1.0) mm long and an understory of appressed trichomes 0.05–0.10 mm long. Leaves subsessile to short-petiolate, the petioles 1.0–1.5 mm long, the mature laminas ovate to elliptic (to obovate), the younger laminas lance-ovate to narrowly elliptic, 3–10 mm long, 1.0–5.5 mm wide, 2–4 times longer than wide, cuneate at base, rounded to acute at apex, the margin flat, ciliate. Inflorescence racemose, 30–70 mm long, the axes pubescent with eglandular trichomes, canescent. Flowers pedunculate, usually borne singly along one (rarely both) side of the inflorescence axes, the peduncles 2.0–4.5 mm long. Bracts narrowly ovate to narrowly elliptic, 2–4 mm long, 0.8–1.5 mm wide, eglandular. Bractlets narrowly elliptic to subulate, 1–3 mm long, eglandular. Calyx 3.5–4.8 mm long, rarely glandular, the lobes 3.0–4.5 mm long. Corolla rose-purple within, (12–) 14–20 mm long, the lobes of the lower lip 3–4 mm long. Stamens 7–9 mm long, the thecae 2.0–2.3 mm long. Style 9–12 mm long. Capsule 8–11 mm long, the head 5–7 mm long. Seeds 3.5–4.0 mm long, 2.5–3.0 mm wide.

Flowering: June to September.

Distribution: Limestone slopes in mesquite scrub, Huasteca Canyon, west-central Nuevo León (Fig. 1).

This species is known only from Huasteca Canyon, an immense limestone canyon southwest of Monterrey, where it has been collected on several occasions. The species is a dominant element of the steep slope vegetation in parts of the canyon.

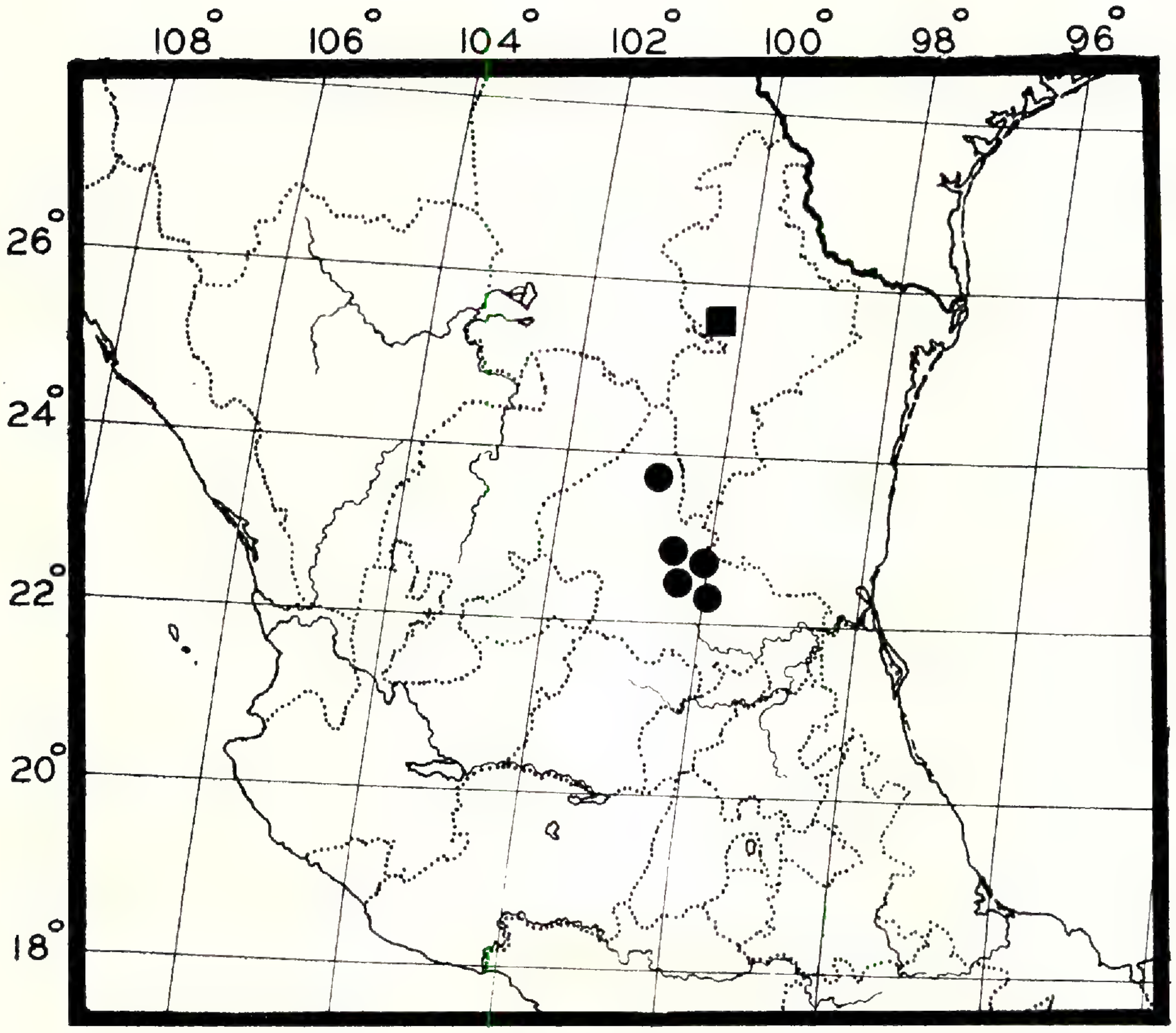

FIG. 1. Distribution of *Mirandea huastecensis* (square) and *M. grisea* (circles).

Little is known concerning the reproductive biology of this species. When plants of *M. huastecensis* were visited during the summer of 1978, fruit production was evident but most of the seeds had been destroyed by insect larvae. The flowers had no detectable fragrance but produced nectar at the base of the corolla tube. Pollination is likely effected by bees or flies which descend the tube for nectar or which feed on the pollen.

Additional specimens examind: Mexico. Nuevo León: Huasteca Canyon, 1.4 mi S of the Centro Recreative La Huasteca, *Daniel 762* (ARIZ, ASU, CHAPA, ENCB, INIF, MICH, MEXU); Huasteca Canyon, *Ward 5715* (DUKE, MICH); above Ranch of Dr. E. Aguirre Pequeno, Canyon de Huastecas, *Kruckeberg 4804* (MICH, NY, UC, WTU): Huasteca Canyon, *LeSueur 413* (F, TEX); Monterrey & Sta. Catarina, *Arsene 6278* (F, MO, US); Huasteca Canyon, *Langman 2919* (US).

Mirandea grisea Rzedowski, Ciencia (México) 19: 80. 1959. Type: Mexico. San Luis Potosí: 20 km. al NW de Cd. del Maíz, *Rzedowski 9464* (MEXU, holotype; MICH!, isotype). Fig. 2.

Younger stems pubescent with appressed trichomes 0.05–0.30 mm long. Leaves petiolate, the petioles 1–3 mm long, the laminas lanceolate to narrowly elliptic (to oblanceolate), 7–20 mm long, 1–7 mm wide, 3–6 times longer than wide, cuneate to obtuse at base, acuminate to acute at apex, the margin revolute, not ciliate. Inflorescence spicate, 20–120 mm long, the axes occasionally glandular. Flowers sessile, opposite at the nodes of the inflorescence axes. Bracts lanceolate to subulate, 4.5–6.0 mm long, 0.8–2.0 mm wide, occasionally glandular. Bractlets subulate, 1.5–3.0 mm long, usually glandular. Calyx 3.5–4.0 mm long, glandular, the lobes 3 mm long. Corolla blue-violet, 11–19 mm long, the

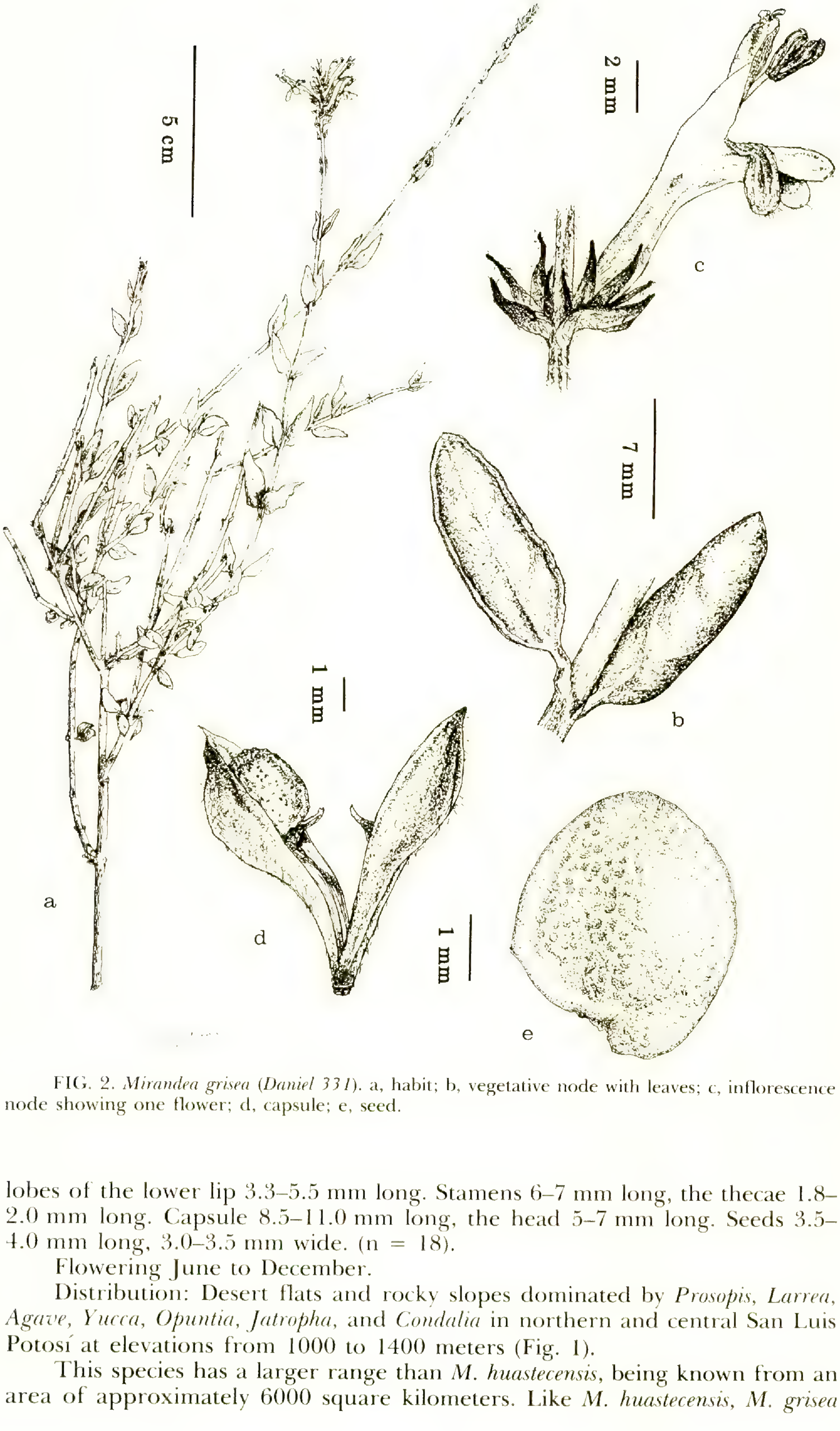

FIG. 2. *Mirandea grisea* (*Daniel 331*). a, habit; b, vegetative node with leaves; c, inflorescence node showing one flower; d, capsule; e, seed.

lobes of the lower lip 3.3–5.5 mm long. Stamens 6–7 mm long, the thecae 1.8–2.0 mm long. Capsule 8.5–11.0 mm long, the head 5–7 mm long. Seeds 3.5–4.0 mm long, 3.0–3.5 mm wide. (n = 18).

Flowering June to December.

Distribution: Desert flats and rocky slopes dominated by *Prosopis, Larrea, Agave, Yucca, Opuntia, Jatropha,* and *Condalia* in northern and central San Luis Potosí at elevations from 1000 to 1400 meters (Fig. 1).

This species has a larger range than *M. huastecensis*, being known from an area of approximately 6000 square kilometers. Like *M. huastecensis, M. grisea*

becomes a dominant element of the vegetation in parts of its range, sometimes forming nearly pure stands of several hundred square meters.

Populations of *M. grisea* visited during the summer and fall of 1978 showed considerable fruit production. The only visitors observed were numerous small, black ants which roamed around the flowers. Abortion of the two anthers was observed in a large proportion of the flowers. Seeds of *Daniel 331* were subsequently grown in a greenhouse at The University of Michigan. The adult plants were partially self-compatible with only a small number of artificially selfed flowers producing fruits.

Additional specimens examined: Mexico. San Luis Potosí: 17.9 mi. E of jct. Hwy. 80 and Hwy. 57, ca. Lat. 22°47′N, Long. 100°15′W, *Daniel 331* (ASU, CAS, DUKE, ENCB, GH, MICH, NY, UC, US); 9.5 mi. SE of El Tepeyac, ca. Lat. 22°35′N, Long. 99°50′W, *Daniel 852* (ASU, F, MEXU, MICH, MO, NY, TEX); 10.6 mi. W of Cd. del Maíz, ca. Lat. 22°30′N, Long. 99°42′W, *Henrickson & Lee 17585* (ASU); eastern San Luis Potosí, *Kenoyer 2394* (GH); cerca de Matehuala, *Paray 2619* (MICH); Duro, SE of Las Tablas, *Pennell 18064* (F, MICH, NY, PH); just E of Huizache Jct., *Pinkava et al. P13537* (ASU, ENCB); 5 km. al SW de Presa de Guadalupe, mpio. de Guadalcázar, *Rzedowski 6760* (MICH); 8 km. al NNW de Santa Ana Pozas, mpio. de Guadalcázar, *Rzedowski 8250* (MICH).

ACKNOWLEDGMENTS

I am grateful to the curators of the herbaria cited in the text for loans of specimens, to Terry Noah for rendering the drawing of *M. grisea,* and to Bruce Parfitt for providing the chromosome count. Field studies were made possible by NSF grant DEB 78-09321.

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Contr. Univ. Mich. Herb. 15:177–179. 1982.

FURTHER NOTES ON *STECCHERINUM CRASSIUSCULUM* (HYDNACEAE)

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Steccherinum crassiusculum Harrison was described from a specimen collected on a fallen log in Jalisco, Mexico in 1960. The junior author obtained two additional collections of this rare fungus from the base of a living *Citrus* cultivar in the central Llanos region of Venezuela during July 1980. The field notes provide the first description of the fresh condition of this taxon.

Steccherinum crassiusculum Harrison. Can. J. Bot. 42: 1207. 1964. Figs. 1 & 2.

Basidiocarps 6–20 cm broad, irregular in outline, surface with low ridges and tufts with numerous shallow depressions, cottony, buff to pinkish buff but dried to dull grayish brown. Margin blunt, sterile, overgrown by brownish tomentum that slightly extends onto the surface, white, bruising yellowish. Context soft, mainly buff but with an upper grayish brown layer and a narrow lower layer concolorous with the spines, fragile after drying. The context of the youngest immature specimen (*Ovrebo 1137A*) after drying was thick, woody, and buff-colored. Spines up to 6 mm long, pinkish flesh-color, close, round or flattened and sometimes divided with two or more tips, grayish after drying and brittle.

The basidiocarps of *Ovrebo 1179A* were attached laterally, with one surrounding a dead twig. In *Ovrebo 1137A*, the single carpophore had a short tapered stipe with a brownish context that darkened downward.

Spores 5.6–7(–8) × 4–4.8 μm, pip-shaped to obovate, slightly inequilateral with finely verrucose walls, ornamentation more distinct with age, walls thin; the SEM photograph (Fig. 1) illustrates the ornamentation as a complex system of uneven ridges and processes forming irregular, partially reticulate patterns. Basidia 30–40 × 8 μm, clavate, hyaline, thin-walled, clamped, with stout sterigmata up to 4.5 μm long. Hyphae of spines 3.5–4.8 μm wide, clamped at most septae, constricted slightly or expanded at the septae. Tramal hyphae up to 8 μm wide, clamped at most septae, with the walls externally ornamented with "oily material" (Fig. 2).

Collections studied: Fundo Pecuario Masaguaral, about 44 km south-southwest of Calabozo, Estado Guarico, Venezuela, 5 July 1980, *Ovrebo 1137A* and 31 July 1980, *Ovrebo 1179A*, both at the base of a *Citrus* tree. (Both collections deposited in MICH; one-half of each collection, *Ovrebo 1137B* and *Ovrebo 1179B* deposited in VEN).

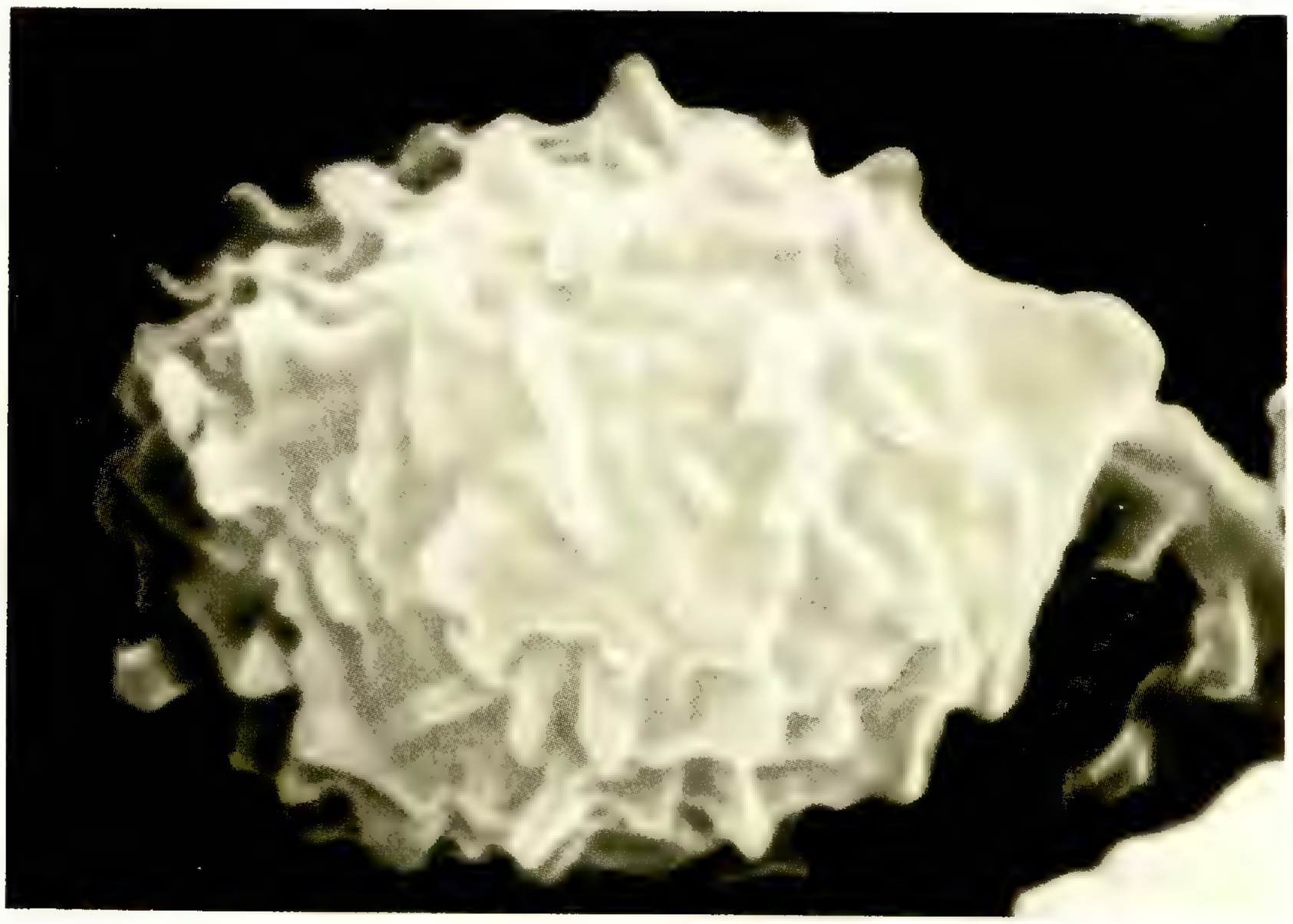

FIG. 1. Spore of *S. crassiusculum* ×10,000 from *Ovrebo 1179A* from Venezuela.

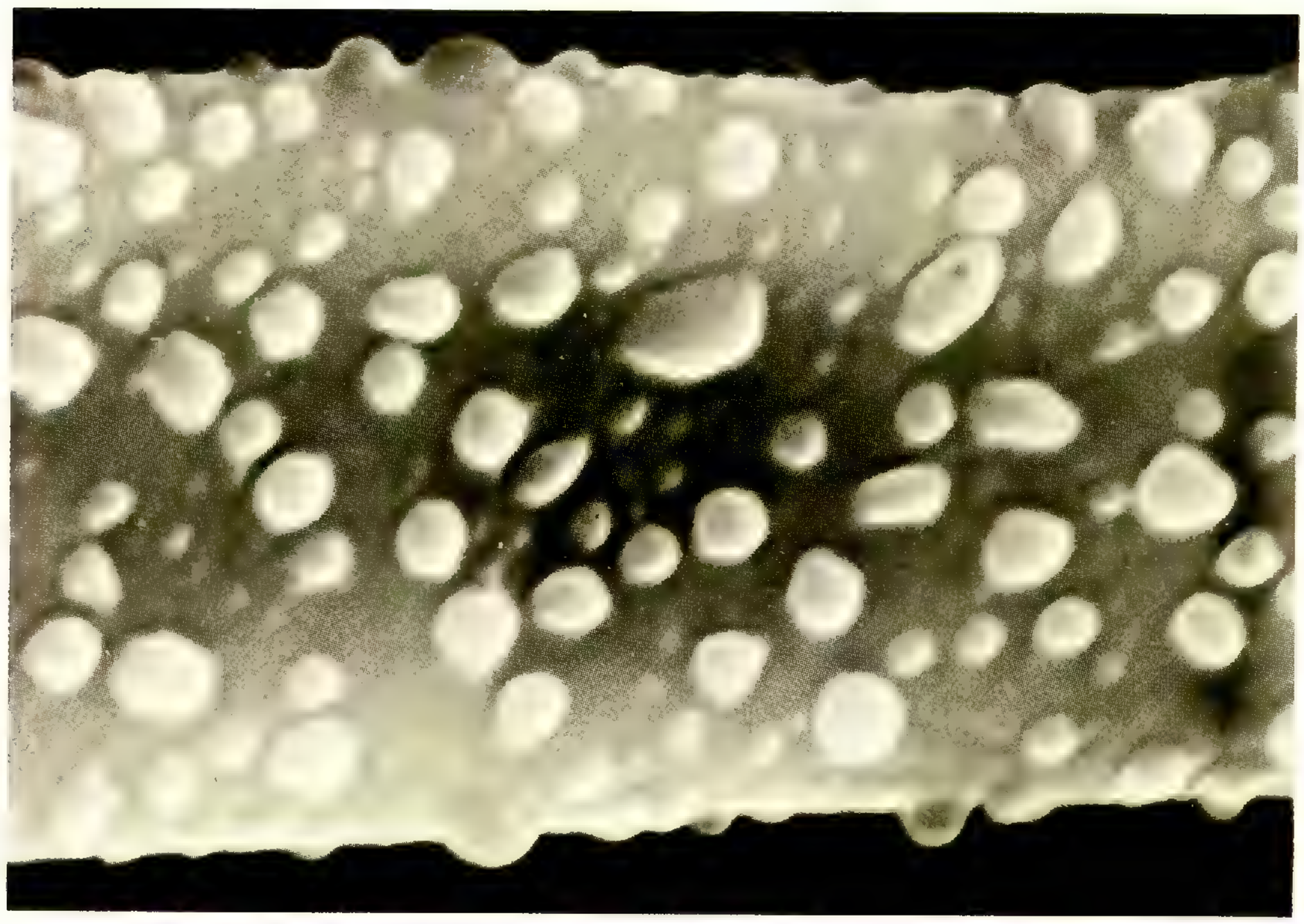

FIG. 2. Droplets on the surface of a hyphal strand of *S. crassiusculum* ×7,000 from *Ovrebo 1179A*.

The three known collections of this species are very different in shape, thickness of context and method of attachment to the substrate but are strikingly similar in details of color of context and pileal appearance.

The microscopic details of the above collections are the same as in the holotype. The peculiar ornamented hyphae found in the holotype when viewed in Melzer's reagent were not as obvious in the above collections. In 2.5% KOH, the oil droplets on the hyphal walls were immediately evident in all collections; however, the droplets in the above collection disappeared rather quickly as compared to the holotype.

ACKNOWLEDGMENT

We thank Tomas Blohm for allowing access to the research site.

Contr. Univ. Mich. Herb. 15:181–190. 1982.

THE NEW SYNANTHEROLOGY VS. *EUPATORIUM* IN NEUVA GALICIA

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For more than a decade, the ivory tower of synantherology has been partially obscured by a cloud. Some researchers believe they can see the sun through the haze, whereas others believe they see a distorted image. The cloud, in the form of a frenetic and almost incredible spate of publications that reminds one inevitably of Rafinesque or Otto Kuntze, has been of special import to students of the tribe Eupatorieae of the Compositae. Between 1967 and 1976 Robert M. King and Harold Robinson published at least 167 papers on the Eupatorieae, mostly dealing with the dismemberment of *Eupatorium* and the realignment of the species in this and related groups. At least 78 new genera were published, and a flood of new combinations in all but forgotten genera like *Ageratina* Spach, *Chromolaena* DC., *Koanophyllon* Arruda da Camara, and *Fleischmannia* Sch. Bip., in which the number of names rose rapidly to about 230, 130, 109, and 75, respectively (cf Heywood *et al.*, 1977, pp. 462–480). As other genera increased in size at the expense of *Eupatorium*, that taxon in the view of King and H. Robinson shrank to a mere 37 or 38 species, and disappeared entirely from the flora of Mexico. From 1977 to 1981, inclusive, King and H. Robinson continued the same work, although at a somewhat diminished pace. In the journal *Phytologia* alone they published at least 52 new papers on the Eupatorieae, and 19 additional new genera, bringing the total number of new and resuscitated genera to well over 100.

Evidently these radical changes in generic concepts need to be examined closely before their substance can be incorporated into a regional treatment like the *Flora Novo-Galiciana* (McVaugh, in press), which of necessity must be conservative. Several kinds of changes are being advocated. Species are being realigned on the basis of new characters, and the taxa to which they belong after realignment are being assigned increasingly to new genera or to genera which for all practical purposes are new because they have not been accepted since publication. Anyone attempting to use the new system is faced with two questions: Are the genera really natural groups? If so, are they sufficiently distinct from one another to justify the elaborate mechanism of setting them up as different genera, with all the species newly named in a way that inevitably obscures their relationships to species in other similar taxa? In the *Flora Novo-Galiciana*, of which the part treating the Compositae should be in press when this article appears in print, the problem is a significant one because the genus *Eupatorium*, in the sense of most botanists from the time of Bentham until very recently, has undergone a hasty but searching review at the hands of King and H. Robinson, with the result that in Nueva Galicia all 68 species have been transferred out of *Eupatorium* into 16 different genera. This article is intended to touch upon some apsects of the arguments for and against the proposed changes.

I have to admit that my philosophical prejudice favors the inclusive generic concept. There are pedagogical advantages in this, partly because of the neces-

sary links between taxonomy and nomenclature. Presumably the primary aim of systematics is to point out relationships and resemblances, and the need to describe differences between taxa should be subsidiary to this. Once a splinter-genus is put forward, its name and the names of all the included species acquire a certain specious permanence (to paraphrase an expression that I think Lincoln Constance once used, "an embalmed finality"). A writer may say "I think group A constitutes a distinctive subgroup of *Eupatorium*," and we are free to study his opinion and accept it or disregard it. If, however, even without any proof, he says "I think group A constitutes a new genus," the names that he proposes will remain forever in the literature, and it will be necessary for others to show conclusive evidence as to why they should not be accepted. I think the burden of proof should be on the other side; proposals for generic segregation should be so clear, forceful, and well-documented that most botanists would be disposed to accept them.

If I have a major criticism of the New Synantherology (King and H. Robinson, 1970a), this is it. It may be true that *Eupatorium* in the sense of Bentham and B. L. Robinson includes a great many different evolutionary lines, but that more than 100 of these lines are to be treated as distinct genera is hardly credible and has not been adequately documented. Such fragmentation of any large genus is possible, but for the most part botanical opinion has been against it. Scores of genera could be made in the same way from *Solanum*, *Euphorbia*, *Eugenia*, *Lobelia*, or *Carex*, to name a few. Sometimes a genus like *Chamaesyce* wavers on the brink of acceptance for many years, in and out of *Euphorbia* as new evidence and opinions are presented, but wholesale transfer of names too often comes from opinion hastily reached without adequate evidence.

In B. L. Robinson's (1913) key to the genera of the Eupatorieae, his preliminary discussion included a statement of the most useful characters by which the genera were separable. Upon failing to find new useful characters, Robinson said, "one is in consequence forced to a restatement of the distinctions of pappus, achenes, anther-tips [appendages], and involucral-bracts [phyllaries] as yielding after all the most practical basis for classification in the group." By the use of Robinson's criteria, the vast majority of the Mexican species with definite anther-appendages, prismatic achenes, and numerous more or less persistent pappus-bristles were placed either in *Eupatorium* (with achenes mostly 5-ribbed or -angled) or *Brickellia* (with achenes commonly 10-ribbed or -angled).

The concept of *Brickellia* has been relatively little changed by modern workers, but recent research suggests that it includes some species with 5-angled achenes, and that its definition depends upon a combination of the characters of narrow tubular corollas, smooth expanded style-branches, broad imbricate strongly nerved phyllaries, an expanded hairy style-base, and a chromosome number of $x = 9$ or 10, with polyploidy rare. King and H. Robinson have advocated the removal of certain groups from *Brickellia* (in our flora, e.g. *Asanthus* and *Steviopsis*), but few species are involved, and *Brickellia* remains almost unchanged except by the addition of one species (*B. pedunculosa*) with 5-angled achenes.

B. L. Robinson's *Eupatorium*, on the other hand, has been stigmatized by King and H. Robinson as "monolithic," and these authors have made a determined effort to bring "some order out of the previous chaos." I do not find among their publications any formal statement as to just how the monolithic *Eupatorium* is artificial, or how it is planned to dismember it, or how it was decided that certain admittedly coherent parts of the complex were to be treated as genera instead of infra-generic taxa. The method of King and H. Robinson, as described in *The New Synantherology*, focuses first on the delimitation of genera through new characters discoverable by the use of the compound microscope. The authors state their opinion that "Synantherology like bryology is most

properly a study for the compound microscope," and they continue, "it is frustrating to see our carefully determined results criticized by people who apparently do not intend to either adequately check them or in fact adequately read them." Among potentially significant characters discussed in this provocative paper, they listed "surface structure of the corolla lobes, cellular structure of the style branches, form and vestiture of the stylar node, cellular structure of the anther appendage, form of exothecial cells, structure of the anther collar, pubescence of the corolla, distribution and structure of setae on the achene, and cellular structure of the carpopodium."

The same authors have published what they call "studies" of most of the eupatorioid genera that they recognize. These "studies" generally consist of a few paragraphs of discussion, a generic description, and a list of the names of the species referred to the genus in question. A few of the earlier studies were adequately documented revisions, e.g. that of *Hofmeisteria* (King, 1967); and of *Decachaeta* (King and H. Robinson, 1969). These are useful papers, because it is possible to use the keys, descriptions, and citations of specimens to test the authors' conclusions. Most of the later papers in *Phytologia*, however, are difficult to use (difficult, in the authors' own words, to "adequately check or adequately read"), because they are mere lists of unverifiable synonyms, with a minimum of discussion, and that often assuming too much on the part of the reader. Probably the most outspoken critic of this work has been B. L. Turner, who said in 1970 (Grashoff and Turner, 1970), "We would like to assume that these resultant genera are more cohesive than was the classical *Eupatorium*. Unfortunately, we are not given more conclusive evidence, in most cases, than that this or the other micro-character is present or absent in an entire group of species. Insomuch as the segregate genera are so poorly defined and defended we await more conclusive evidence based on a more well-balanced taxonomic inquest." In the same vein Turner continued, "The most responsible and competent work which can be done in this tribe . . . must therefore involve itself with information concerning living plants, their ecology, pollination biology, genetics and evolution. One can attempt to correlate micro-characters with this background."

Parenthetically it may be added here that King and H. Robinson, in their more recent papers, have made an effort to include cytological and chemical data, but apparently have not yet demonstrated their taxonomic significance throughout the Eupatorieae. It seems to be well-established that in *Brickellia* and its relatives, $x = 9$, whereas in the major genera segregated from *Eupatorium*, the prevailing number is $x = 10$ or $x = 16, 17$, with polyploidy not uncommon (Turner, 1978).

No general synopsis of the King–H. Robinson system of the Eupatorieae has yet been published. A discussion with non-comparative summaries of 19 sub-groups[1] including lists of genera in each was published in Heywood *et al.* (1977, chapter 15). From a study of the summaries it seems clear that the authors have given full consideration both to the "classical" morphological characters, and to microscopic characters, but it is difficult to compare one group satisfactorily with another. For example, consider the essential statements on the Eupatoriinae and the "*Ageratina* group," including the genera *Eupatorium* and *Ageratina*, respectively:

Eupatoriinae: "This typical element of the tribe is characterized by sub-imbricate involucral bracts and by pubescent style bases. Some of the species in various genera have apical cells of the pappus rounded or bulbous at the tip. The corolla lobes are smooth and sometimes have stomata. [Some] genera of the

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[1]These "sub-groups" were ultimately accepted by King and H. Robinson as subtribes. Valid names were provided for them as needed (King & Robinson, 1980).

group have distinct annular thickenings in the cells of the anther collar, [others] lack these thickenings" (Heywood *et al.*, 1977, p. 454).

Ageratina group [later called Ageratinae Less.]: "The relatives of *Ageratina* and *Oxylobus* are distinct among the groups with higher chromosome numbers by the eximbricate to weakly subimbricate involucral bracts and by the papillose inner surfaces of the corolla lobes, [which] are smooth only in parts of the specialized genus *Piptothrix*. Style bases are always glabrous; and they are usually enlarged, except in *Pachythamnus, Standleyanthus, Spaniopappus* and a few species of *Ageratina*. The pappus is usually capillary and often easily deciduous, but it is reduced in a few taxa. . . . The tube of the corolla is usually long and often very slender. The anther collars are elongate with many subquadrate non-annulated cells" (Heywood *et al.*, 1977, p. 460).

All this, for the sake of useful comparison, reduces to the following: style-bases pubescent in *Eupatorium*, glabrous and usually enlarged in *Ageratina*, assuming that these genera have the group-characters; corolla-lobes smooth vs. papillose on the inner surfaces; cells of the anther-collar sometimes with annulated thickenings, vs. cells non-annulated. On the strength of such few really positive differences, and the want of attention to other contrasts, if any exist, it is easy to question the validity of such generic segregation and the generic groupings that are proposed as a result.

It is true that the accounts of the generic groupings in chapter 15 of Heywood *et al.* (1977) are necessarily brief. The prescribed format does not permit the use of keys, nor of much discussion of individual genera. I therefore turned to King and H. Robinson's treatment of the Eupatorieae in the *Flora of Panama* (D'Arcy *et al.*, 1975), which is the only other major published exposé of the opinions of these authors, and to their "studies" of *Ageratina* and *Eupatorium* (King & Robinson, 1970c; 1970b). From these it becomes apparent that *Ageratina*, with its more than 230 species, is in effect the core-genus of the *Eupatorium*-complex in Latin America; it seems to be what is left after all the more specialized taxa have been pulled out of the classical *Eupatorium*. It is described as having the anther-appendages longer than wide; the corolla-lobes papillose within, usually short-hairy and sometimes glandular without, smooth without, longer than wide; style usually with a distinct basal enlargement, glabrous; cells of anther collars without distinct annular thickenings in walls; pappus bristles often fragile and deciduous, their apical cells pointed; carpopodium distinct with prominent upper rim; achenes usually setose but not glandular. In contrast, *Eupatorium* proper is treated as a north-temperate genus of 37 or 38 species, almost entirely absent from tropical America. In the same year (King & H. Robinson, 1970c), in the discussion preliminary to the listing of almost 200 new combinations in *Ageratina*, the authors stated, "*Eupatorium* clearly differs from *Ageratina* by its smooth corolla lobes, hairy stylar base, indistinct carpopodium, presence of only glands [i.e. not with both hairs and glands] on the corolla and achene, and blunt-tipped pappus setae [i.e with apical cells blunt]."

Here then is a direct comparison between the principal genera of the Eupatoriinae and the Ageratinae, as these groups were contrasted in Heywood *et al.* (1977). Here we have the additional information that the carpopodium is indistinct in *Eupatorium*, vs. distinct in *Ageratina*; the pappus-bristles have the apical cells obtuse in *Eupatorium*, but acute in *Ageratina*; the achenes are glandular in *Eupatorium*, but usually setose but not glandular in *Ageratina*. Some of these characters require close observation, but it does not take a compound microscope to make them visible.

Upon tabulation of these and other features, it transpires that *Eupatorium*, *sensu* King and H. Robinson, has a unique combination of several characters: Anther-collars broad, apical cells of pappus-bristles blunt, style-base hairy, caropodium none, geographical range mostly extra-tropical. This situation is

analogous to that in the genus *Lobelia* (Campanulaceae), a group of several hundred species, mostly tropical, but with 25–30 species in eastern North America and one in Europe having a unique type of foveolate-reticulate seed found nowhere else in the genus. It is evidently a monophyletic group, but as far as I know there has been no serious attempt since the 17th century to set it off from the rest of the species as a distinct genus.

Here one is tempted to ask, what useful purpose is served by treating such groups as genera? Is there reason to think the difference in the shape of cells at the tip of the pappus bristles indicates a major evolutionary discontinuity? Or the form of cells on the surfaces of the corolla-lobes? As Grashoff and Turner said in the article quoted above, it seems likely that many micro-characters are under very simple genetic control. It may be wishful thinking to suggest as do King and H. Robinson (1970b), that "the great majority of species that have been placed in *Eupatorium* obviously have no close relationship with this group."

In connection with the segregation of other genera, it may be instructive to examine the schemes used by King and H. Robinson in the *Flora of Panama*, and in a key to the genera of Eupatorieae of Nueva Galicia (1972). In both these treatments an interesting discrepancy becomes apparent. Though micro-characters are listed for each genus, they are not handled comparatively in a way to suggest that they have been any more important in the delimination of genera than the familiar old characters of pappus, anther-appendages, and phyllaries. In the parts of the generic keys that include taxa with pappus of 10 or more capillary bristles (i.e. the classical *Eupatorium* and a few other genera), the first major segregations are a genus marked by having the mature phyllaries all deciduous (*Chromolaena*), a group of genera in which the anther-appendages are short and wider than high (in Nueva Galicia, *Decachaeta, Eupatoriastrum, Koanophyllon*), and a group in which the style-bases are hairy (mostly *Brickellia*). At the next major couplet in the keys, two large genera (*Ageratina, Fleischmannia*) are contrasted with the remaining groups because the corolla-lobes are papillose, not smooth, on the inner surface. Among the genera with smooth corolla-lobes, the first one taken off is *Neomirandea*, marked by its epiphytic habit and broad quadrate corolla-cells. Subsequent leads in the key depend upon the enlargement or lack of it in the style-base, the shape of the base of the achene, the persistence or lack of it of the inner phyllaries, the details of pubescence and glandularity of the corollas and achenes, the number of flowers in the head, and the presence or absence of pellucid dots in the leaves.

One is forced to conclude that the "new" characters utilized by King and H. Robinson (not all "micro-characters" by any means), have provided some useful indication about species-groups in *Eupatorium, sensu lato,* but in no way have they confirmed the bold assertion made in *The New Synantherology* that the compound microscope would provide a panacea. The authors of the article may indeed be correct in saying that [by the use of microscopic data], "future determinations can be made with an ease and accuracy not previously possible," but they have not yet shown convincingly that any new combinations of characters indicate real generic differences. It still remains a matter of opinion whether the "monolithic" genus *Eupatorium* is better broken up or not.

In the eupatorioid gene-pool in Nueva Galicia, I visualize a generalized taxon from which others have been segregated because of extraordinary unit characters, or combinations of such characters with other macro- and micro-characters. Plants in this generalized imaginary taxon have opposite leaves, relatively few-flowered heads (flowers seldom more than 50), involucre of 20–50 somewhat imbricate phyllaries in 2–4 (–5) series, receptacle flat or convex, sometimes hairy, anther-collars narrow with quadrate cells below, the walls inornate or nearly so, the anther-appendages longer than wide, the style glabrous without basal enlargement, the carpopodium distinct, the pappus of (5–) 20–40 bristles

with acute apical cells. For the sake of convenience, call this the "*Ageratina*-complex."

Take this generalized taxon, made the corolla-lobes papillose, enlarge the basal node of the style (usually), make the achenes setose but not glandular, the exothecial cells in the anther longer than wide (usually), and the pappus-bristles fragile, and you have *Ageratina*. In Nueva Galicia this includes well over half the species of the classical *Eupatorium*.

Take away the carpopodium, make the heads smaller, with fewer and shorter flowers, and let some of the species have smooth corolla-lobes, and you have *Piptothrix*. In the past a useful distinction between *Piptothrix* and *Eupatorium* (*sensu lato*) has been supposed to be in the number of pappus-bristles (ca 15 or less, vs. 20 or more), but I cannot find any discussion of this among the papers of King and H. Robinson.

Begin with the generalized taxon, make the corolla-lobes papillose, the achenes *usually* setose but not glandular, the exothecial cells *mostly* quadrate or wider than long, the pappus-bristles *sometimes* fragile, and the cells of the anther-collars elongate with distinct annular thickenings, and you have *Fleischmannia* (*sensu latissimo*). King and H. Robinson, 1970c, p. 209) state that some species of *Fleischmannia* are superficially similar to species of *Ageratina*, but they continue, "we do not consider them at all closely related. *Fleischmannia,* while similar in habit, leaf form, and tendency for hairy corollas, is clearly distinct in the papillose backs of the corolla lobes, the strongly annulated thickenings of the anther collars, the complete lack of enlargement of the style base, and the thick-walled cells of the strongly rimmed carpopodium. Even the papillae of the inner surface of the corolla lobes are different in basic structure, being only the projecting upper ends of elongate cells and not forming a compact mass. Needless to say the more specialized features of *Ageratina* such as the narrow stemmed corollas and very deciduous pappus setae do not occur in *Fleischmannia*."

In this instance combinations of micro-characters play a major role in the separation of moderately large groups of species which are otherwise not very different. How does one assess the evolutionary importance of annulated thickenings on the cells of the anther-collars? Until more is known about such things, would it not be more realistic to restrict *Fleischmannia* to the one original species (in which the pappus consists of 5–6 bristles only), and leave the other 75 or so miscellaneous species in *Eupatorium?* This situation may be compared with that in the very large tropical genus *Eugenia* (Myrtaceae). In different species there is a bewildering variety of flower-parts pubescent or papillose or glabrous on one side or the other or both, combined in various ways with hard, soft, fleshy or woody fruits, deciduous (because of abscission-layers) or persistent styles and calyces. Most of these are characters directly related to differences in cell-structure, i.e. to micro-characters. Most of the micro-characters have not been analyzed as such, but that seems irrelevant. The point is that here such characters in combination serve to distinguish between species, not genera.

Leaving for the moment the larger "genera" that are delimited by means of combinations of micro-characters, it is necessary to consider other groups that seem to depend chiefly upon a single rather more obvious character.

In Nueva Galicia these include *Neomirandea* (1 species in our area, 24 or more in all), and *Chromolaena* (9 species in Nueva Galicia, over 130 in all). The former is marked especially by its fleshy stems and epiphytic habit; in our species the corolla is hairy inside and the stylar node is enlarged, but in another subgenus the corolla is hairless inside, and the style is not enlarged. In addition to the distinctive habit, species of *Neomirandea* are said to be marked also by the "smooth to slightly bulging, lax cells of the corolla which are very broad and straight-walled in all but a few species; the short carpopodium with small to rather large thin-walled cells; and especially the very elongate inornate anther collars."

The species of *Chromolaena* are notable for having the phyllaries all deciduous in age, leaving the receptacle naked; the corolla-lobes are said to be papillose, and the cells of the anther-collars banded. It may be remarked that in Mexico the woody species assigned to *Chromolaena* are drawn from two superficially very different groups, the section *Cylindrocephala* (*sensu* B. L. Robinson), with cylindrical involucres, and section *Subimbricata*, with shorter, often thistle-shaped, involucres. According to King and H. Robinson these constitute two subgenera, having the corolla-lobes papillose and smooth, respectively, on the inner surface. The corolla-character is not completely correlated with involucre-shape; the character that holds these groups together would seem to be the deciduous habit of the phyllaries, taken in conjunction with the banded anther-collar.

It is easy to accept the premise that groups of two or three species may be "monophyletic" or "homogeneous," and therefore candidates for generic status, even if having but a single character that marks them as different. Larger groups, like *Chromolaena*, are a little different, even if as by King and H. Robinson they are shown to enjoy several characters in common. Is it demonstrable that they are monophyletic? For example, *Chromolaena collina* and *C. odorata* are so different in the form of the involucre that they would never be confused; they are in fact assigned by King and H. Robinson to different subgenera. Certainly it is suggestive that these two species and many others share the characters of deciduous phyllaries, corolla-lobes papillose without, and banded cells of the anther-collars, but it might be urged that this combination has resulted from convergent evolution. Is there any reason to think that differences in cell-shape on one side or the other of the corolla-lobes indicates a major evolutionary line, even if the character is correlated with some others? Thus I should argue as I did above that King and H. Robinson have performed a service to systematics by pointing out the easy accessibility of many characters that have previously been ignored or overlooked, and the fact that some characters occur in combinations with other more obvious characters, but their task is not yet finished. They need to demonstrate, convincingly enough to dissolve a consensus that has persisted more than a century, that combinations of small differences, even if microscopic, can over-ride a profusion of similarities that are apparent to the unaided eye.

A genus revived by the authors of *The New Synantherology*, and said to include more than 100 species, namely *Koanophyllon*, has in the main the characters of the generalized taxon that I like to call the "*Ageratina*-complex," but it has one peculiar attribute; it is "particularly distinctive in its usually short often somewhat reflexed anther appendage with a distinct median groove running up the inner surface." This matter of the shape of the anther-appendage is not diagnostic in the Eupatorieae. According to H. Robinson and King (in Heywood *et al.*, 1977), the appendage "seems to show strong disposition to reduction in the tribe." The same authors list genera in which the appendage is shortened or lacking, in 9 of the 19 groups (i.e. subtribes) that they recognize. It may be supposed that the character is not a strong indicator of taxonomic relationship. It is shared by *Decachaeta* and *Erythradenia*, both of which are referred by H. Robinson and King on other characters to the "*Hebeclinium* group," and by *Koanophyllon* and *Eupatoriastrum* of the "*Critonia* group." The anther-character is not mentioned as one of the distinctive features of either group. One may ask why it is important enough to stress as a generic character. It is an easily observable character, but if it occurs in so many different groups, why not in *Eupatorium*? In spite of the fact that *Decachaeta* and *Koanophyllon* are assigned to different groups [subtribes], it is hard to find a distinction between them (i.e. from published descriptions) except that in the former the leaves are alternate (except in one species), and the receptacle is hairy (in most species).

Many of the smaller "genera" represented in Nueva Galicia are mere satellites, consisting of one or few species each, picked off the surface (so to

speak) of the *Ageratina*-complex or (to coin another name) the *Koanophyllon*-complex, because of some special characteristic. Examples of these include *Erythradenia* (one species in which the pappus is so short as to remain undetected except under careful scrutiny, but which otherwise is much like *Decachaeta*); *Pachythamnus* (one species with stems leafless at flowering time); *Neohintonia* (one species with mostly 1–flowered heads, very short anther-appendages, a carpopodium, and glandular stylar appendages); *Dyscritogyne* (two species with stipitate-glandular achenes); *Kyrsteniopsis* (about four species in all, one in Nueva Galicia, with yellowish flowers—very unusual in the Eupatorieae—and very short filaments); *Conoclinium* (three species, one in Nueva Galicia, with conical receptacle, papillose corolla-lobes, thickenings in the cell-walls of the anther-collars, glandular indument of the corolla and achene, and blunt-tipped apical cells of the pappus-bristles).

In a somewhat larger genus, *Critonia* (more than 30 species, three in Nueva Galicia) the leaves are pellucid-dotted and the corolla-lobes are smooth. Another taxon referred as a genus to the "*Critonia* group" [i.g. Critoniinae] is *Eupatoriastrum* (three species, one in Nueva Galicia), which has short anther-appendages, many-flowered heads, and chaffy receptacles. This last feature, as I noted in 1972 (McVaugh, 1972, p. 388), seems to have developed in various eupatorioid lines, and is not a very dependable generic character.

Satellite genera like the above are not difficult to recognize, even without a compound microscope. They are obviously different in some special way from their relatives; presumably they represent twigs on the evolutionary tree. Whether or not they are distinct enough to deserve to be given generic status, with all the complications this entails, is still a matter of opinion. It is difficult to prove beyond question that *Neohintonia monantha* constitutes its own genus, and is not just a species of *Eupatorium* with 1–flowered heads. As B. L. Turner (1978, p. 344) recently said, one needs "compelling reasons" for the elevation of "this or that 'exceptional' species" to generic rank. Perhaps thorough monographic study will confirm some such generic segregations in the future, but in the pages of a general work like the *Flora Novo-Galiciana* it seems out of place to obscure genuine similarities between species by putting different names on whole series of minor variants when so little is known about the development and causes of the variation.

A large regional flora, like the *Flora Novo-Galiciana*, should remain useful, and reflect contemporary opinions, for as long as possible after publication. In a situation like the one under discussion, the author is confronted by a dilemma. Regardless of his course of action, his work, or parts of it, may become obsolete almost at once because of generic concepts that are not in accord with contemporary opinions. Every systematist knows that opinions about generic limits go more or less in cycles; few American botanists in 1980 accepted J. K. Small's view, as expressed in 1933, that *Acer* comprises five genera.

The treatment of the *Eupatorium*-complex in the *Flora Novo-Galiciana* may come to be regarded as reactionary, assuming that the generic concepts of King and H. Robinson are not accepted in that work, but come to be widely known (and perforce used) elsewhere in tropical America because of extended treatments in other regional floras. On the other hand, unless the concept of a multi-generic *Eupatorium*-complex gains general acceptance in the next few years, any author that uses it may find that instead of climbing onto the bandwagon he has climbed into the tumbril. I think it is possible to avoid both.

SUMMARY AND CONCLUSIONS

There is no *a priori* reason why *Eupatorium* should be broken up, merely because it is too large to be easily understood. There is no limit on the size of

genera. Botanical consensus of at least the last two centuries is that within most large generic complexes there may be ill-defined infra-generic taxa that continue to defy precise definition, and do not constitute independent genera except in the opinion of some extremists. It is also the consensus that large genera—especially those that have survived taxonomic study over long periods—are not likely to be hiding multitudes of very small or monotypic genera in their ranks. Thus it seems highly probable, even without knowledge of the facts, that carving scores of small new genera out of the "monolithic" *Eupatorium* does not correctly represent the evolutionary picture. Such a multitude of satellites is so unusual, not only in the Compositae but in flowering plants generally, that it is at once suspect. To use the example I used above, *Eupatorium monanthum* may be a very unusual species of *Eupatorium,* but to set it up as a separate genus over-emphasizes the differences between it and related species, and glosses over the similarities.

When it comes to the proper disposition of larger groups of species within a great generic complex, there is still no final test. One always must ask, What are the diagnostic characters? Are they strong or weak characters? How many are correlated? In the case of segregate genera, are the resulting groups homogeneous? Is the case for segregation strong enough to permit us to over-ride traditional usage, which is the historical expression of botanical opinion?

I find it difficult to be completely objective about these questions as they apply to the genera of the New Synantherology. No other authors known to me in modern times have proposed such sweeping reorganization of a major plant group in such a short time, and asked the public to take so much of it on faith, without much documentation. I do not doubt their integrity, but I suspect that in their haste to get new generic names on everything, they have given no more than perfunctory attention to many species. They have promised a full presentation of their views in published form, and I can only hope that it will come soon. In the meantime I hold to the views expressed above, that Robert M. King and Harold Robinson have provided a significant stimulus to future work on the taxonomy of the Eupatorieae; they have pointed out new and valuable diagnostic characters (though perhaps overstating the value of such characters even for their own work); they still need to present their full data in a way that will show their proposed genera as units in perspective against the whole picture of the classical *Eupatorium.* I see no reasonable course at the moment except to treat *Eupatorium* in the *Flora Novo-Galiciana* in the traditional sense.

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COMPOSITARUM MEXICANARUM PUGILLO SUPPLEMENTUM

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The five taxa that are newly described in the following pages are all based on material that was received too late for inclusion in an earlier paper, *Compositarum Mexicanarum Pugillus* (Contr. Univ. Michigan Herb. 9: 359–484. 1972). The comments and new names in this paper, like those in the earlier one, are presented as a necessary preliminary to a treatment of the Compositae for a proposed *Flora Novo-Galiciana*. The scope of the flora was discussed in the 1972 paper and in other sources cited there. The part of the flora dealing with the Compositae (volume 12) is in press as this paper appears in print. The drawings for figures 1–4 were made by Karin Douthit.

Verbesina pietatis McVaugh, sp. nov. Fig. 1.

Perennis, herbacea, 1–1.5 m alta, caulibus exalatis foliosis annuis, inflorescentia excepta simplicibus, e rhizomate lignoso nudo oriundis; folia ramique alterni; inflorescentia sparse hispidula, caulis versus basin glabrescens; folia supra scabrida, subtus scabridula venis pilosis, pilis rigidis acutis erectis; phyllaria dense strigosa; folia elliptica, penninervia, 8–10 cm longa, 2.5–4 cm lata, apice acuta, basi acuta vel cuneata, sessilia, vel petiolo crasso nudo 3–5 mm longo; folia superiora sensim minora; margines laminarum saepe revolutae, ut videtur integrae sed dentibus crassis callosis remotis instructae; capitula pauca subumbellata, terminalia pedunculis 5–8 mm longis suffulta, cetera (2–6) pedunculis adscendentibus approximatis 2–5 cm longis, vel pedunculis 1–2 elongatis ramosis 2–3-cipibus; capitula radiata, 2.5 (–3?) cm lata (radiis extensis mensa), fructu subglobosa, 1.5 cm lata; phyllaria ca 20, intima (flores radii 11–15 subtendentia) elliptica vel ovata, acuta, 4–5 mm longa, 1.5–2 mm lata, submembranacea; phyllaria exteriora pauca, crassiora, subfoliacea, usque ad 7 mm longa, 4 mm lata; flores radii flavi, pistillati, ut videtur fertiles, ligulis ellipticis, extus pubescentibus, 8–10 mm longis, 4–5 mm latis, tubo ca 1.5 mm longo piloso; achaenia radii epapposa vel aristis brevibus 1–2 instructa, nigrescentia, 2.5 mm longa, sparsim strigosa, 3- vel 5-angularia vel plana; flores disci multi (plus quam 100), corollis flavis 4 mm longis, tubo crasso piloso 1 mm longo vel ultra, faucis cylindricae vel anguste infundibuliformis venis sparsim pilosis, lobis ca 0.7 mm longis, pilis paucis grossis instructis; antherae nigrescentes ca 2 mm longae, basi minute auriculatae, appendicibus pallidis ovatis 0.5 mm longis; styli rami 1.2–1.3 mm longi, apicibus deltoideis applanatis; achaenia (paullo immatura) valde applanata marginibus attenuatis, atrofusca, e basi ad apicem utrinque alata, apice emarginata, corpore glabro, sagittato-obovato, 3–3.5 mm longo, 1.7–1.9 mm lato, alis membranaceis, ciliatis, distaliter latioribus (usque ad 0.7 mm latis) erosisque, ultra corporis in auriculas 0.5–0.8 mm prolongatis; aristae pappi plerumque 2, ad alas non adnatae, longior 1 mm longa adscendens tenuis antrorse barbata, alia plerumque brevior; squamellae nullae; paleae 5–6 mm longae, base lineari conduplicata, parte distali latiore, strigosa, in cuspidem pallidam acutam recurvatam terminanti.

FIG. 1. *Verbesina pietatis* (*Rzedowski & McVaugh 504*, type). Portions of flowering plant, × 0.5; flowering head with facing ray removed, × 2.5; ray-flower, and disk-flower, × 5; slightly immature disk-achene, × 10; pale, × 5; abaxial view of style-tip, greatly enlarged.

Among the perennial herbaceous yellow-rayed species of *Verbesina* with wingless stems and alternate leaves, this one is distinctive because of the relatively broad harsh elliptic leaves ca 3 times as long as wide, the stout woody horizontal rhizomes, and the recurved tips of the pales. The species with which it might be confused in the key, namely those of the *V. oxylepis–parviflora–hypomalaca* complex, are more pubescent and quite different in appearance, with oblong to lanceolate or linear leaves mostly 5–15 times as long as wide, the stems from a short woody caudex, and the pales with erect tips.

MICHOACAN: Cerro Grande de Cujaruato, SW of La Piedad, rocky summits in sparse oak forest, 2500 m, flowering 16 Nov 1971, *Rzedowski & McVaugh 504* (MICH, the type). Otherwise unknown.

It seems strange that such a conspicuous plant should have remained so long undetected in the mountains of the Central Plateau of Mexico, where narrow endemism is not the rule. It may transpire that an earlier name is available for it. The mountain on which it occurs, however, is a very isolated forested peak rising high above the surrounding grassland, and supporting a flora including dense stands of a shrubby species of *Ceanothus* which is unknown anywhere else in this part of Nueva Galicia.

Verbesina curatella McVaugh, sp. nov. Fig. 2.

Frutex usque ad 2 m altus, ramis foliisque oppositis, pilis brevibus multicellularibus cavis dense obsitus; rami exalati, pilis sordidis vel nigricantibus flaccidiusculis 0.5–1 mm longis crebre obsiti; folia rigida, supra ad modum *Curatellae* perscabra, subtus scabriuscula, reticulata, venis venulisque crebre pilis pallidis acutis erectis obsitis; laminae penninerves, ellipticae vel ovatae (vel summae obovatae), 12–20 cm longae, 5–8 cm latae, apice obtusae vel subacutae, basi longe cuneatae, quasi sessiles, marginibus calloso-dentatis; ramos foliosos corymbi compacti parvibractaeti, 10 cm lati, 7 cm longi, ramulis oppositis, terminantes; capitula discoidea, fructu ca 2 cm lata, 1.3 cm alta, sub anthesi ut videtur campanulata, basi obtusa, 1.3 cm alta; pedunculi crassi 2–10 mm longi; phyllaria ca 11–13, imbricata, dense brevipilosa, plusminusve 2–3-seriata, exteriora (4–5) carnosiuscula, ovata, 2–3 mm longa; alia usque ad 5–6 mm longa, 2–3 mm lata, oblongo-elliptica, obtusa; intima in paleas transientia et achenia sterilia subtendentia; flores disci ca ?35–55, corollis flavo-viridibus, 5.5–6.5 mm longis, fere cylindricis, tubo angustiore dense piloso, fauce longa glabra, lobis pilosis 0.7–1 mm longis; antherae nigrescentes 2–2.5 mm longae, appendicibus parvis triangularibus 0.3–0.5 mm longis; styli ramuli ca 2 mm longi, apicibus attenuatis; achenia plana, late obovato-deltoidea, e basi ad apicem alata, 5.5–8 mm longa, corpore 2.5–3 mm lato, verrucoso, strigoso, alis pallidis paullo suberosis, distaliter latioribus usque ad 3 mm latis, prope marginibus strigosis, apice truncatis vel supra achaenium productis, ad bases aristarum erectarum subulatarum 2 subaequalium, 4–6 mm longarum adnatis; squamellae nullae; paleae oblanceolatae, conduplicatae, 7–11 mm longae, apicibus dense pilosis fuscatis, encrassatis, paullo cucullatis.

JALISCO: Mpio. de Cabo Corrientes, above El Tuito, road to Mina del Cuale, rocky stream-valleys in region of pine-oak forest, the valleys with *Podocarpus*, oaks, and other deciduous trees, 850–1150 m, fruiting 16–19 Feb 1975, *McVaugh 26438* (MICH, type).

Unknown except from the type, this is distinctive among the shrubby species of *Verbesina* with discoid heads because of its harshly scabrous (whence the epithet *curatella*) ovate to obovate leaves, the dense sordid or blackish pilosity of the branches, and the large heads with numerous disk-flowers.

FIGS. 2–4. *Verbesina* and *Stevia*. *Verbesina curatella* (upper row of figures, from the type, *McVaugh 26438*). Portion of stem with cauline leaves, × 0.5; disk-achene, × 3.5; disk-flower, × 4; portion of inflorescence-branch, × 0.5; pale, × 4. *Verbesina villaregalis* (middle figures, from the type, *Puga 5744*). Leaves at base of inflorescence, and cauline leaf below, × 0.5; slightly immature achene, × 3.5; head slightly before anthesis, from below, × 3.5; pale, × 4. *Stevia zacatecana* (lower figures, from the type, *McVaugh 25940*). Portion of stem with cauline leaves, and terminal portion of inflorescence before anthesis, × 0.5; involucre from over-mature inflorescence, × 5; achene, × 10.

Verbesina villaregalis McVaugh, sp. nov. Fig. 3.

Ut videtur frutex vel arbor (partes basales ignotas), *V. culminicolae* similis; inflorescentia capitulaque fere ut in *V. culminicola*; rami alterni vel subalterni, foliorum basibus alati, alis initio viridibus, nonnunquam linearibus, decurrentibus 1–1.5 cm longis, sed plerumque valde corrugatis, 5–8 mm longis, 2–4 mm latis; partes vegetativae pallide pubescentes pilis appressis, sed folia subtus glauca et glabra (secus costam pilis sparsis exceptis); folia anguste oblongo-lanceolata, lateribus fere paralellis; laminae 10–15 cm longae, 1–1.5 cm latae, 6–10 (–15)-plo longiores quam latiores, remote et non profunde serrato-denticulatae, basi subcordatae vel late rotundatae, e basi sensim ad apicem longiacutum attenuatae; folia majora inflorescentiae basi petiolis 1–2 mm longis; flores disci corollis 2.5–3 mm longis; antherae ca 1.5 mm longae, nigrescentes, pallide striatae; achaenia disci obovato-sagittata, alis inclusis 3.5 mm longa, 2 mm lata; paleae 4–4.5 mm longae, cuspide terminali maturitate plusminusve recurvato-uncinata.

Species Luz María Villarreal de Puga, Instituti Botanici Universitatis Guadalajarae Praeceptricis, grate nominavi.

JALISCO: Mpio. de Mascota, between Cerro del Molcajete and Laguna de Juanacatlán, in pine-oak forest, 1800–2110 m flowering 30 Dec 1973, *Luz Ma. Villarreal 5744* (MICH, the type). (Sra. de Puga's name appears on most of her herbarium labels as Luz Ma. Villarreal, but she informs me that she would prefer to have her collections cited under her married name of Puga, so the foregoing should be cited as *Puga 5744*).

Among the shrubby species of *Verbesina* with small yellow radiate heads, alternate and decurrent leaves or winged stems, this one may be confused with other supposed endemics in western Jalisco, e.g. *Verbesina culminicola* and *V. glaucophylla*. In the latter, at least in the type, the heads are discoid, but this may not be a fundamental character. None of the three species is sufficiently known, and their relationships need to be investigated further. From *V. culminicola*, *V. villaregalis* may be separated as follows:

1. Leaves green beneath, long-tapering to base, 1.5–3 cm wide, 4–7 times as long as wide; petioles 5–10 mm long or the upper shorter; tips of pales hooded with erect points. *V. culminicola.*
1. Leaves glaucous beneath, abruptly rounded at base, 1–1.5 cm wide, (6–) 10–15 times as long as wide; longest petioles at the base of the inflorescence 2 mm long; tips of the pales with recurved points. *V. villaregalis.*

Verbesina parviflora (H.B.K.) Blake, var. **zacatecana** McVaugh, var. nov.

Perennis, herbacea 20–65 cm alta, simplex vel ramis paucis alternis adscendentibus, caulis exalatis, foliis linearibus alternis vel inferioribus oppositis, capitulis radiatis longe pedunculatis; flores radii ca 8, pistillati sed ut videtur steriles; flores disci numerosi (50–?75); achaenia alata, obovata vel suborbicularia; paleae membranaceae, apicibus rectis acutis; a var. *parviflora* foliis linearibus 3–7 mm latis, 10–15-plo longioribus quam latioribus differt.

ZACATECAS: Summits between Jalpa and Tlaltenango, ca 35 km W of Jalpa, in open oak forest, 2500 m, in fruit 23 Oct 1970, *Rzedowski & McVaugh 1044* (MICH, the type); ca 10 km S of Tlaltenango, near Telesteipa, rocky terrain in oak forest, in flower 13–14 Jul 1976, *S. Correa 123* (MICH), *140* (MICH).

This plant seems not to differ in any obviously significant way from typical *Verbesina parviflora* except in the width of the leaves. In var. *parviflora,* which ranges from Chihuahua and northern Nayarit to San Luis Potosí, the leaves are (6–) 10–15 (–20) mm wide, 3–6 times as long as wide. Apparently this narrow-leaved plant of Zacatecas represents a local population of the more widespread upland species.

Stevia zacatecana McVaugh, sp. nov. Fig. 4.

Frutex ramosus 1 m altus, fere glaber, foliis junioribus sparsim pilis flaccidis ad venas obsitis; inflorescentia grosse stipitato-glandularis; folia, et rami (inflorescentiae eis inclusis) oppositi; folia triplinervia, firmiuscula, in siccitate paullo nitida, subtus pallidiora, utrinque dense globulis resinosis obsita; folia caulinia principalia 4–8 cm longa, (0.5–) 1–2 (–2.5) cm lata, ovato-lanceolata, apice obtusa vel subacuta, basi cuneato-attenuata, petiolo indistincto marginato, vel usque ad 0.5–1.5 cm longo; laminae utro latere dentibus 5–7 non profunde crenato-serratae; venae majores valde adscendentes, subtus prominulae, venis ceteris inconspicuis; inflorescentia pedunculata, glomerulis paucis compactis 1–2 cm longis latisque, ramulis patentibus, bracteis angustis; capitula cylindrica, 6–7 mm longa, subsessilia, cum bracteis pedunculisque valde glandulosa; corollae (maturae non visae) glabrae; alabastra sparsim apice stipitato-glandulosa; achaenia homomorpha linearia 3.5–3.8 mm longa exaristata, angulis intervallisque minute hispidula; pappus coroniformis vix 0.2 mm longus.

ZACATECAS: Summit ridges between Jalpa and Tlaltenango, steep humid ravines in montane oak forest, 2550 m, with inflorescences developing 24 Jan 1975, *McVaugh 25940* (MICH, holotype, and isotype).

Known only from the type locality, where very abundant on the high sheltered forested slopes near the flat summits. First seen in December 1970, when all the plants were sterile, and again, sterile but putting out new leafy shoots, in October 1973 (*Rzedowski & McVaugh 962,* ENCB, MICH). Probably the height of the flowering season is in March or April.

This is evidently a member of the group of species that B. L. Robinson (The Stevias of North America. Contr. Gray Herb. II. 90: 90–159. 1930) called subseries *Fruticosae,* and J. L. Grashoff (A systematic study of the North and Central American species of *Stevia.* Ph.D. dissertation, University of Texas. pp. i–xiv, 1–609. Austin, 1972) called series *Fruticosae.* The plants are real shrubs with stems persisting more than one season. There are about 25 species, all according to Grashoff completely sexual, many with the pappus reduced to an awnless crown in all the achenes. Grashoff contrasts eight species in which (as in *S. zacatecana*) the achenes are hispid and the corolla-lobes glabrous. Of these one is white-tomentose, and three normally have aristate achenes. Of the remaining four, *Stevia lucida, S. nelsonii, S. salicifolia,* and *S. subpubescens,* none has the combination of copiously stipitate-glandular inflorecence, essentially glabrous plant-body, and consistently opposite branching in the inflorescence clusters.

Contr. Univ. Mich. Herb. 15:197–204. 1982.

THE FERNS OF STEERE AND HARRINGTON

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In 1870, soon after graduating from the University of Michigan, Joseph Beal Steere (1842–1940) began a more than five year expedition around the world. Despite traveling mostly alone, often experiencing great hardship, and frequently being exposed to grave peril, his accomplishments in natural science on this expedition were so extraordinary that he was awarded an honorary Ph.D. by the University of Michigan even before his return to Ann Arbor. It was the first degree of this kind granted by the University. Although Steere made other scientific trips and went on to a notable career as Professor of Zoology, specializing in Ornithology, and was also curator of the University Museum from 1876 to 1894,[1] he remains best known for the explorations, research, and natural history collections made from 1870 to 1875 (Gaige, 1932).

Steere obtained botanical materials from Brazil, Peru, Ecuador, China (including Taiwan and Hong Kong), the Philippines, and what is now part of Indonesia (the Moluccas). His collections, made without numbers, were divided into over 2,500 specimens (Harrington, 1875), virtually all of which were pteridophytes; these were later treated as consisting of 241 taxa (Harrington, 1877). For his entire natural history collection, Steere eventually received $4,500 from the University of Michigan, along with an agreement to his stipulation that the material be forever known as the "Beal and Steere Collection" (Steere, 1879).

Although Steere's mother was a Beal, and he was a first cousin of the accomplished Michigan botanist William James Beal,[2] the reason for the inclusion of the name Beal was that the expedition was financed by Rice A. Beal, a wealthy relative and the publisher of the Ann Arbor "Courier," a weekly newspaper. In return for this aid, Steere authored 96 letters for publication in the newspaper, periodically reporting on his experiences and observations. These well-composed and information-filled letters conferred upon Steere a modicum of fame; selected letters were republished shortly before his death (Steere 1938a, 1938b).

During Steere's absence, a close friend and fellow graduate from the Class of 1868, Mark Walrod Harrington (1848–1926), rose to the position of Assistant Professor, with botany his main interest, and it befell Harrington to identify the botanical specimens, nearly all ferns, received from the expedition. It is plausible that the numerous fern specimens were secured by Steere as a special favor to Harrington, who had already been working with ferns, and whose list of 200 fern species in the University of Michigan herbarium (previous to the Steere

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[1]Steere's resignation and early retirement, in 1894, resulted from what was considered a too forceful advocacy of prohibition (Crum, 1977).

[2]Another notable botanist in the immediate family is the bryologist William Campbell Steere, grandson to J. B. Steere.

collections) was published by the Board of Regents (Harrington, 1875). When he traveled to Germany in 1876, Harrington brought the Steere ferns with him, and identified them during a side-trip to the Royal Botanic Gardens, Kew, England, with help from J. G. Baker, the resident pteridologist. The study resulted in the first substantial botanical paper associated with the University of Michigan (Harrington, 1877), and in the election of Harrington as a Fellow of the Linnean Society of London.

But Harrington soon switched fields, and by the time he returned to Ann Arbor in 1879, he had spent two years in Peking as an astronomer. He headed the Astronomy Observatory at the University of Michigan until 1891, when he moved on to be the first chief of the United States Weather Bureau. In 1895 he accepted the post of President at the University of Washington, which he held for only one year. In 1899, soon after the publication of his book *All About Weather*, Harrington suddenly disappeared; when finally located he was suffering from partial amnesia. The last 27 years of his life were spent wandering as a hobo, working as a logger and day laborer, and as a patient in a mental institution (Jones, 1978; Baker-Blocker, 1980).

Harrington presumably transported the entire fern collection to Kew (K) in 1876 for his study. After naming it, he left a duplicate set for Kew and shipped the remainder, unaccompanied, back to Ann Arbor (MICH), from where further duplicates were distributed to at least five institutions: Field Museum (F), Harvard University (GH), Missouri Botanical Garden (MO), Smithsonian Institution (US) and Yale University (YU). Very probably the task of distributing the duplicates was assumed by Elizabeth C. Allmendinger, author of an enumeration of the flora of the Ann Arbor area, a friend of Harrington, and a volunteer assistant in the University of Michigan herbarium. As partial compensation for her volunteer work she was allowed to select duplicate specimens for her own personal herbarium (Voss, 1978); she made herself an incomplete set of fragments of the Steere ferns. The Allmendinger herbarium was donated to MICH by her estate in 1928. An additional set of fragments was detached from the MICH specimens in 1907 and sent to E. B. Copeland in the Philippines, forming the basis of two published papers (Copeland 1908; 1936). These fragments were returned in 1958 when Copeland's herbarium of about 25,000 sheets was purchased by the University of Michigan for $16,000. Thus MICH now possesses three sets: the original and by far the most ample set, and partial sets from Allmendinger and Copeland.

From Steere's pteridophyte collections, Harrington[3] described as new nineteen ferns, fifteen species and four varieties; of these, eleven were from the Philippines and four each from Taiwan and Peru. One problem arising from these has been uncertainty as to whether specimens at K or specimens at MICH should be designated lectotypes. Since Harrington apparently had all the specimens with him when he wrote his descriptions and since none of the collections of the new taxa seem to be mixtures, the problem is mainly of formal technical significance. Nevertheless, the type system requires that a designation be made. Although Harrington certainly decided which taxa to describe as new while he was at K and published in a British journal, it is my opinion that all the lectotypes (with one exception, *Adiantum steerei* Harr.) should be the MICH specimens, and in this paper I make that designation. The specimens at K are therefore isolectotypes.

Of the arguments in favor of MICH, the first is that MICH was the home institution for both Steere and Harrington, and the specimens selected by an author for his home institution should generally be given preference.

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[3]No one after Harrington has made a J. B. Steere plant a type.

Secondly, information about some of the K specimens of the type collections, kindly supplied by Dr. R. E. Holttum, reveals that those at MICH are superior by being generally more ample or useful; we can be virtually certain that Harrington returned to MICH what he considered to be the best specimens. For example *Nephrodium subpedatum* Harr. was described from only two fronds, of which just one was said to be fruiting, i.e., fertile. The fertile frond is at MICH.

Thirdly, and again with the help of Dr. Holttum, I have ascertained that the K sheets have less detailed annotations than the MICH specimens,[4] and do not have the original field notes. Rather, in at least one case, that of *Lomaria areolaris* Harr., the K sheet fails to provide any indication of the very unusual habitat, which is written on the MICH sheet in Harrington's hand and also appears with the published description.

A fourth consideration is that the MICH specimens of Steere's collections are named directly on the sheets in Harrington's hand and Steere's field notes were rewritten by Harrington either directly on the sheets or on mechanically reproduced handwritten labels.[5] This raises the possibility that the information may have been written by Harrington before leaving MICH or while at K, which might then indicate that he had pre-selected the Michigan sheets, although he did retain an interest in botany after turning professionally to astronomy,[6] and did some herbarium work after 1879 (Mains, 1956).

Finally, according to Steenis-Kruseman (1950, p. 504), only 170 Steere ferns were acquired by K. If this number is accurate, it would confirm the fact that the K set is quite incomplete and certainly not the best set.

In the following re-evaluation of the Harrington types, I have provided the original citation, all nomenclatural synonyms, and the name(s) accepted by current authors. Two of the ferns have until now been generally misinterpreted: *Nephrodium subpedatum* Harr. and *Polypodium steerei* Harr. I have also given the fullest possible information of locality and date, in some cases obtained from the manuscript of Hubbell (1964) who reconstructed the itinerary from Steere's letters. The sequence of ferns in Harrington's publication, placing the New World collections last even though made first, otherwise followed that of *Synopsis Filicum* (Hooker & Baker, 1868); that same sequence is followed here.

THE NEW TAXA

Hymenophyllum thuidium Harr., J. Linn. Soc. Bot. 16: 25. 1877; Copel. Philip. J. Sci. 64: 116, pl. 56. 1937.

Mecodium thuidium (Harr.) Copel., Philip. J. Sci. 67: 20. 1938.

Lectotype: Philippines, Panay, Iloilo Prov., mountains above Maasin, Jan. 1875, *Steere s.n.* (MICH).

Currently accepted names: *Hymenophyllum thuidium; Mecodium thuidium; H. reinwardtii* v.d.B.; *M. reinwardtii* (v.d.B.) Copel.

The type of *H. thuidium* is at one extreme of variation of the plants associated with *H. reinwardtii*, differing from the latter species as narrowly construed by the much more pronounced and finer crisping of the lamina, narrower and more crowded segments and smaller stature, but certainly not clearly distinct.

This was grouped by Morton (1968, p. 167, 172) with the species treated as *Meringium* by Copeland on the basis of the toothed margins, but the indusial

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[4]Although one K specimen, that of *Gymnogramma calomelanos* var. *denudata* Harr., bears a locality not on the MICH sheet.

[5]For a sample of Harrington's early writing, see McVaugh (1970, p. 220).

[6]While in China, Harrington himself collected a few plants, including at least one fern, *Cheilanthes argentea* (Gmel.) Kunze, which came to MICH in 1928 with the Allmendinger hebarium.

structure and the form of the receptacle show an unmistakable affinity to *Mecodium*.

Hymenophyllum fraternum Harr., J. Linn. Soc. Bot. 16: 26. 1877 (non Presl 1843).

H. steerei C.Chr., Ind. Fil. 368. 1905.

Lectotype: Philippines, Panay, Iloilo Prov., mountains above Maasin, Jan. 1875, *Steere s.n.* (MICH).

Currently accepted names: *Hymenophyllum fimbriatum* J.Sm. ex Hook.; *Mecodium fimbriatum* (J.Sm. ex Hook.) Copel.

According to Harrington this was found growing with the preceding, and there was only a single plant. The lectotype (or holotype if no other separate specimen was originally made) has a length of rhizome with only a single frond, from which a single pinna that had been detached for study by Copeland is now mounted on a separate sheet.

Davallia philippinensis Harr., J. Linn. Soc. Bot. 16: 27. 1877.

Microlepia philippinensis (Harr.) Copel., Polyp. Philip. 56. 1905.

Tapeinidium philippinense (Harr.) C.Chr., Ind. Fil. Suppl. 3: 176. 1934.

Lectotype: Philippines, Luzon, Mt Mahayhay (= Mt Banahaw), June–July 1874, *Steere s.n.* (MICH).

Currently accepted name: *Tapeinidium luzonicum* (Hook.) Kramer.

Having not seen the sheet at MICH, which had been misfiled, Kramer (1968, p. 552) was only able to cite the specimen at K, although not explicitly as lectotype.

Lomaria areolaris Harr., J. Linn. Soc. Bot. 16: 28. 1877.

Blechnum areolare (Harr.) Copel., Polyp. Philip. 90. 1905.

Stenochlaena areolaris (Harr.) Copel., Philip. J. Sci. 2C: 406. 1908.

Lectotype: Philippines, Luzon, Mt Mahayhay (= Mt Banahaw), growing in the leaves of a *Pandanus*, June–July 1874, *Steere s.n.* (MICH).

Currently acepted name: *Stenochlaena areolaris*.

This is the most unusual of the ferns collected by Steere, and it is also rather strange that his collection of it was the first, since the same area had been previously combed for ferns by, among others, Cuming and Brackenridge. The fern is a scandent epiphytic aquatic, rooting in and clambering between the water-filled leaf bases of *Pandanus simplex* Merrill, which is common in the area and even cultivated. The pandan is the mainstay of an important cottage industry, its long leathery leaves being woven into mats, baskets, hats and other articles. The leaf bases contain a substantial amount of water and harbor an interesting fauna, including small crabs. Plant-held waters were termed phytotelmata by Maguire (1971), although *Pandanus* was not mentioned. My observations are that prothallia only develop in leaf pockets not already inhabited by the *Stenochlaena*, possibly indicative of allelopathy. The tips of the rhizoids of prothallia develop into branched and expanded holdfasts anchored to the sides of the pocket that may function to help prevent the gametophytes from being flooded out in the frequent heavy rainstorms such as characterize the vicinity of Mt Banahaw.

Asplenium steerei Harr., J. Linn. Soc. Bot. 16: 28. 1877.

Lectotype: Philippines, Luzon, Mt Mahayhay (= Mt Banahaw), epiphytic on trunks, June–July 1874, *Steere s.n* (MICH).

Currently accepted name: *Asplenium steerei*.

While reducing *Asplenium benguetense* Hieron. to *A. steerei*, Price (1974a) suggested that *A. steerei* might in turn have to be reduced to one of three earlier

names: *A. acutiusculum* Bl., *A. anisodontum* Presl, or *A. insiticium* Brack. That idea is now withdrawn.

Asplenium acutiusculum Bl. Enum. Pl. Jav. 178. 1828 (Holotype: Java, *Blume s.n.*, L sheet no. 908,311–892) is a smaller individual of the same species as *A. longissimum* Bl. published on the same page (Holotype: Borneo, collector unknown, L sheet no. 922, 167–1020). I here designate *A. longissimum* the accepted name for the species when the two names are combined. For a modern description of the species, see Holttum (1955).

The Philippine *Asplenium anisodontum* Presl based on *Cuming 128* is a member of the complex of *A. caudatum* Forst.; the Hawaiian *A. insiticium* Brack. seems to be a large elaborate form of *A. contiguum* Kaulf. None of these are closely related to *A. steerei.*

Nephrodium luerssenii Harr., J. Linn. Soc. Bot. 16: 29. 1877.

Aspidium luerssenii (Harr.) Christ, Bull. Herb. Boiss. 6: 193. 1898 (non Doerfler, 1890).

Dryopteris luerssenii (Harr.) C.Chr., Ind. Fil. 276. 1905.

Lectotype: Philippines, "Bulukai Island," 1874, *Steere s.n.* (MICH).

Currently accepted names: *Thelypteris ligulata* (Presl) Ching; *Pneumatopteris ligulata* (Presl) Holtt.

Harrington localized this as from "Bulukai Island," and the labels on sheets I have seen read "Bulukai, Luzon," and "Buluka Island, Luzon," but there was and is no such place name. I am convinced that Bulukai Island is a misrendering of Balabac Island from Steere's original field label, long discarded. There is also another possibility. On 23 June 1874, on the first day of his journey on foot from Mahayhay to Mauban, Luzon, Steere reached the "village of Bulukon" and could have found this plant in that vicinity. I agree with the supposition of Hubbell (1964) that "Bulukon" in that case must have been the town of Lucban.

Unable to examine the MICH specimen, which had been misfiled, Holttum (1974a; 1982) cited only a K specimen, but not specifically as lectotype.

Nephrodium eatonii var. **formosanum** Harr., J. Linn. Soc. Bot. 16: 29. 1877.

Lectotype: Taiwan, Keelung, March 1874, *Steere s.n.* (MICH).

Currently accepted name: *Ctenitis eatonii* (Bak.) Ching.

Nephrodium bakeri Harr., J. Linn. Soc. Bot. 16: 29. 1877; Bak. in J. D. Hook. Icon. Plant. 17: pl. 1664. 1886.

Dryopteris bakeri (Harr.) Copel., Philip. J. Sci. 2C: 405. 1907.

Haplodictyum bakeri (Harr.) Ching, Sunyatsenia 5: 251. 1940; Holtt. Kalikasan 2: 63. 1974.

Cyclosorus bakeri (Harr.) Copel., Gen. Fil. 142. 1947.

Thelypteris bakeri (Harr.) Reed, Phytologia 17: 262. 1968.

Pronephrium bakeri (Harr.) Holtt., Fl. Males. II, 1: 516. 1982.

Lectotype: Philippines, Panay, Iloilo Prov., mountains above Maasin, Jan. 1875, *Steere s.n.* (MICH).

Currently accepted names: *Thelypteris bakeri; Haplodictyum bakeri; Pronephrium bakeri.*

Haplodictyum, when recognized as a genus, consists of four species, all endemic to the Philippines (Holttum, 1974b).

Nephrodium subpedatum Harr., J. Linn. Soc. Bot. 16: 30. 1877.

Aspidium subpedatum (Harr.) Diels, Natur. Pflanzenfam. 1(4): 186. 1899.

Tectaria subpedata (Harr.) Ching, Sinensia 2: 23, t.4. 1931.

Lectotype: Taiwan, E. of Takao (= Kaohsiung), March 1874, *Steere s.n.* (MICH).

Currently accepted name: *Tectaria polymorpha* (Wall. ex Hook.) Copel.

Ching (1931, p. 23) published a photo of the "type" but, instead of a Steere specimen, it is the type of a name that is based on a later Morse collection from the China mainland and that Ching assumed to be synonymous. In Flora of Taiwan (DeVol et al. 1975), this species will key out to *Tectaria trifolia,* a synonym of *T. angulata* (Willd.) Copel. However, I have seen no specimens referrable to *T. angulata* from Taiwan and I believe that all so named are *T. polymorpha*; for the distinctions, see Price (1974b, p. 45).

Harrington noted that only one of the two fronds collected was fertile, and it is the fertile frond that is present at MICH, thus supporting the choice of the MICH specimens as lectotypes of the Harrington names, rather than those of K.

Polypodium aoristisorum Harr., J. Linn. Soc. Bot. 16: 30. 1877.
Nephrodium aoristisorum (Harr.) Copel, Polyp. Philip. 28. 1905.
Dryopteris aoristisora (Harr.) C.Chr., Ind. Fil. 252. 1905.
Cyclosorus aoristisorus (Harr.) Copel., Gen. Fil. 142. 1947.
Thelypteris aoristisora (Harr.) Reed, Phytologia 17: 260. 1968.
Nannothelypteris aoristisora (Harr.) Holtt., Blumea 19: 38. 1971; Kalikasan 2: 65. 1974; Fl. Males. II, 1: 538. 1982.

Lectotype: Philippines, Panay, Iloilo Prov., mountains above Maasin, Jan. 1875, *Steere s.n.* (MICH).

Currently accepted names: *Thelypteris aoristisora; Nannothelypteris aoristisora.*

This species provides the type of the generic name *Nannothelypteris,* which, like *Haplodictyum* (see *Nephrodium bakeri* above), applies to several diminutive species endemic to the Philippines (Holttum, 1974b).

Polypodium schenkii Harr., J. Linn. Soc. Bot. 16: 31. 1877.

Lectotype: Philippines, Panay, Iloilo Prov., mountains above Maasin, Jan. 1875, *Steere s.n.* (MICH).

Currently accepted names: *Ctenopteris obliquata* (Bl.) Copel.; *Prosaptia obliquata* (Bl.) Price, infra.

The types of *Ctenopteris, Cryptosorus,* and *Prosaptia* all belong to a natural species-group of Grammitidaceae characterized by pinnatifid or just pinnate fronds, with sori impressed or sunken into the lamina, and with rhizome paleae clathrate and ciliate. The earliest generic name for these is *Prosaptia,* and thus *Ctenopteris* as a genus name cannot stand despite its current wide use. The proper combination for this species is: **Prosaptia obliquata** (Bl.) Price, *comb. nov.* (basionym: *Polypodium obliquatum* Bl. Enum. Pl. Javae 129. 1828).

Polypodium craterisorum Harr., J. Linn. Soc. Bot. 16: 31. 1877.

Lectotype: Philippines, Luzon, Mt Mahayhay (= Mt Banahaw), June–July 1874, *Steere s.n.* (MICH).

Currently accepted names: *Ctenopteris celebica* (Bl.) Copel.; *Prosaptia celebica* (Bl.) Tag. & Iwats.

This species is rather unusual among Grammitidaceae by having the stipes conspicuously articulate; they join short, broad phyllopodia.

Polypodium hammatisorum Harr., J. Linn. Soc. Bot. 16: 32. 1877.

Lectotype: Philippines, Luzon, Mt Mahayhay (= Mt Banahaw), June–July 1874, *Steere s.n.* (MICH).

Currently accepted name: *Crypsinus pyrolifolius* (Goldm.) Copel.

Although collected by Steere "on fallen timber," the usual habitat of this fern is high on small branches and twigs in mid-mountain and mossy forest.

Polypodium steerei Harr., J. Linn. Soc. Bot. 16: 32. 1877.
Microsorium steerei (Harr.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 4: 306. 1933.

Lectotype: Taiwan, Takow (= Kaohsiung), Ape's Hill, Oct. 1873, *Steere s.n.* (MICH).

Currently accepted name: *Microsorium punctatum* (L.) Copel.

Although the name *M. steerei* is accepted in Flora of Taiwan (DeVol et al. 1975), this plant is only an inconsequential form of the wide-ranging and variable *M. punctatum.*

Drymoglossum carnosum var. **obovatum** Harr., J. Linn. Soc. Bot. 16: 33. 1877.

D. subcordatum var. *obovatum* (Harr.) Bak., J. Bot. 28: 267. 1890.

D. obovatum (Harr.) Christ, J. de Bot. 19: 73. 1905.

Lemmaphyllum microphyllum var. *obovatum* (Harr.) C.Chr., Dansk Bot. Arkiv 6(3): 47. 1929.

Lectotype: Taiwan, Tamsui (This was wrongly published as Posia by Harrington. It is evident from the herbarium labels that he interchanged, by error, the localities of var. *obovatum* and var. *subcordatum,* next on the same page), Dec. 1873, *Steere s.n.* (MICH).

Currently accepted name: *Lemmaphyllum microphyllum* Presl.

Christensen (1929, p. 47) cited the type as *Steere 487* (US), but this must be a misinterpretation of a stray number, as none of the ferns bore collection numbers.

Adiantum steerei Harr., J. Linn. Soc. Bot. 16: 34. 1877.

Lectotype: Peru, Dep. Amazonas, Poma Cocha, 1872, *Steere s.n.* (K, chosen by Tryon, Cont. Gray Herb. 194: 176. 1964).

Currently accepted name: *Adiantum ruizianum* Klotzsch.

This is the only case where one cannot really argue for making a MICH specimen the lectotype. Harrington cited two different collections in the original publication, both from northern Peru, one from Poma Cocha and the other from between Moyobama & Chachopoyas. From between these syntypes, Tryon (1964) chose the Poma Cocha specimen at K and, as the first to choose, he must be followed. There is no Poma Cocha specimen now at MICH, it apparently having been sent off for exchange (Tryon cited isotypes at GH, MO, and US). Three sheets remain at MICH, two from between Moyobamba & Chachapoyas, and one labeled Castia, Peru.

Polypodium xantholepis Harr., J. Linn. Soc. Bot. 16: 36. 1877.

Lectotype: Peru, between San Bartolomeo & San Mateo, Oroya-Linia R.R., March 1873, *Steere s.n.* (MICH).

Currently accepted name: *Polypodium xantholepis.*

This is close to *P. thyssanolepis* A.Br. ex Klotzsch, but is somewhat smaller; the paleae of the lamina below are darker and more strongly clathrate, and the upper surface glabrous.

Polypodium laevigatum *var.* **rigidum** Harr., J. Linn. Soc. Bot. 16: 36. 1877.

Lectotype: Peru, Dep. Amazonas, Rio Utcubamba, July 1872, *Steere s.n.* (MICH).

Currently accepted name: *Campyloneuron phyllitidis* (L.) Presl.

The lectotype bears the following unpublished habitat data: "Dry places on rocks and branches."

Gymnogramma calomelanos var. **denudata** Harr., J. Linn. Soc. Bot. 16: 37. 1877.

Lectotype: Peru, 1872, *Steere s.n.* (MICH).

Currently accepted name: *Pityrograma calomelanos* (L.) Link.

Tryon (1962, p. 60) said the "isotype" at K was localized as Pebas, Peru, which Steere visited in Jan. 1872, but that name is not mentioned in the original

publication nor does it appear on the two sheets at MICH. Tryon (1964, p. 68) listed the "type" at K but did not explicitly make it the lectotype.

ACKNOWLEDGMENTS

I am appreciative of the help of Howard Crum (MICH), R. E. Holttum (K), Kenneth Lester Jones (MICH), A. A. Reznicek (MICH), Mary Steere (Ann Arbor), William C. Steere (NY), and Edward G. Voss (MICH).

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Contr. Univ. Mich. Herb. 15:205–207. 1982.

LINUM MCVAUGHII, A NEW SPECIES FROM MEXICO

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A specimen of *Linum*, collected in the state of Jalisco, Mexico, was recently sent to me for examination by Rogers McVaugh, well known for his studies of the flora of Mexico. His surmise that it might represent a new species was correct, in my opinion, and I take considerable pleasure in describing it and naming it in his honor. The following description is based on the single collection.

Linum mcvaughii C. M. Rogers, sp. nov.

L. mexicano affine, sed inflorescentia ramis patentibus, caule porcis suberosis, foliis comparate parvis et numerosis, stylis longioribus et fere omnino connatis.

Coarse, glabrous perennial herb or semishrub, ca 90 cm tall; stem up to 5 mm in diameter and somewhat irregularly corky-rigid below; leaves simple, entire, subcoriaceous, mostly opposite, occasionally whorled below, the uppermost and bracts frequently alternate, all sessile or subsessile, ovate to subcordate, the largest 15 mm long, 7 mm wide, gradually reduced in the inflorescence, also smaller and more dense at the bases of flowering branches and on non-flowering branches; stipular glands present; inflorescence many-flowered, paniculate, more or less leafy, with spreading branches; sepals five, ca 3 mm long, ovate, entire or with a few delicate marginal teeth; petals five, yellow, oblanceolate, ca 10 mm long; stamens five, ca 10 mm long, very closely appressed to the style, with very slender intervening staminodia less than 1 mm long; anthers narrowly elliptic, 1.5–2 mm long; styles five, ca 10 mm long, united nearly to the summit; stigmas capitate; mature fruits and seeds not seen.

Holotype: *R. González T. 466,* 30 Sept., 1971. Alt. 1520 m, bosque de encino y pino en ladera de cerro, entre Cuale y Minas de Oro, Municipio de Talpa, Jalisco, Mexico (MICH).

The new species is illustrated in Fig. 1. It is clearly closely related to a group of three known species, *L. orizabae* Planch., *L. guatemalense* Benth. and *L. mexicanum* H.B.K. (Rogers, Brittonia 20: 107–135, 1968). Of the three it most closely resembles the last. *Linum mexicanum* is also the only one of the three which is so far known from Jalisco. The locality for *L. mcvaughii* lies outside the known range of *L. mexicanum,* however. Fig. 2 shows the distribution of the two species. *Linum mcvaughii* differs from *L. mexicanum* in having corky-ridged stems, more spreading inflorescence branches, smaller, more numerous leaves and longer stamens and styles, the former more closely appressed to the style and the latter united to a greater degree, nearly to the summit.

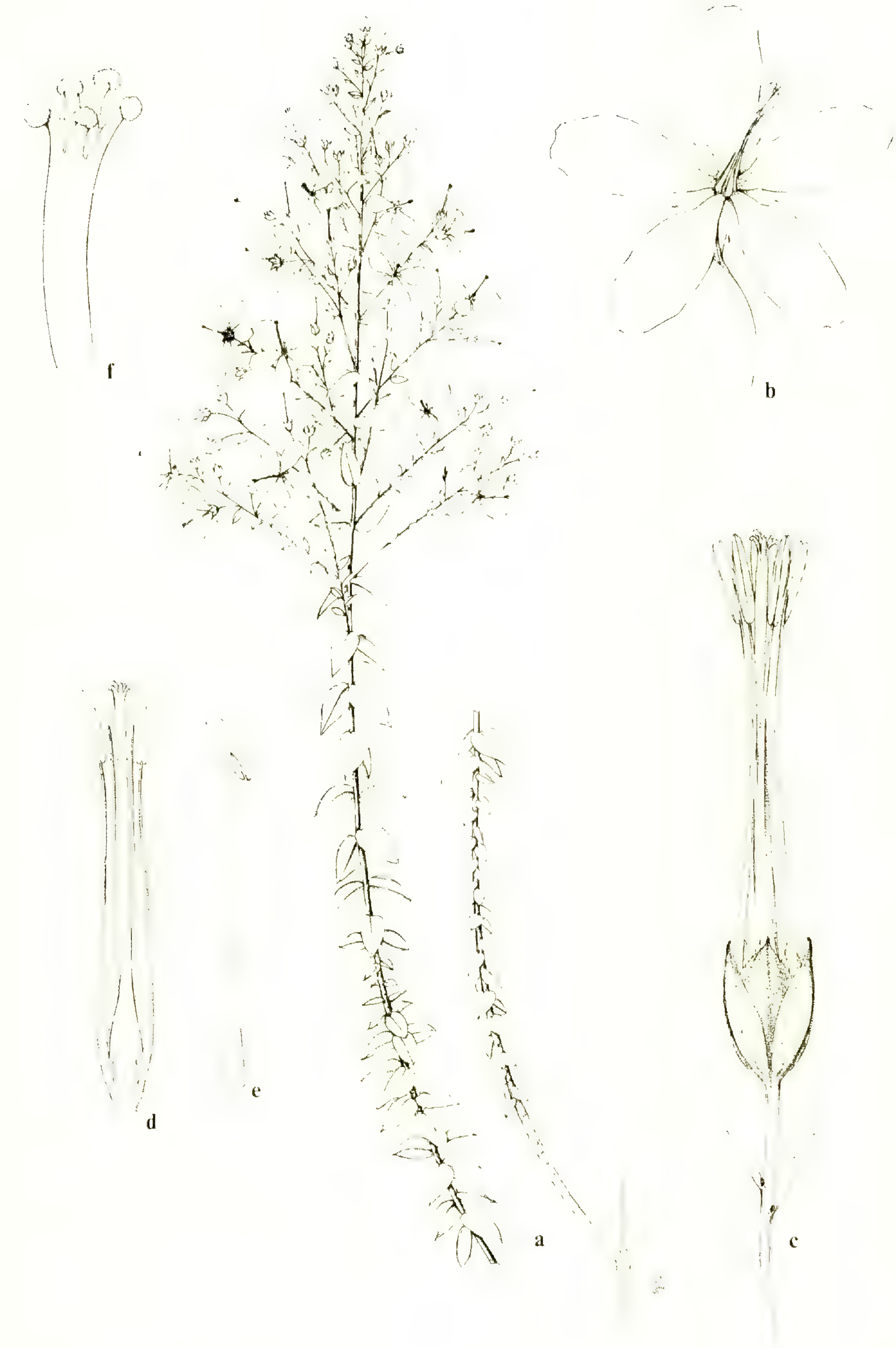

FIG. 1. *Linum mcvaughii*, drawn from the type by Karin Douthit. a, flowering branch × 0.5; b, flower × 2.5; c, old flower with petals fallen × 6; d, androecium and gynoecium × 5; e, anther × 5; f, stigmas × 25.

FIG. 2. Distribution of *Linum mexicanum* (circles) and *L. mcvaughii* (triangle).

Contr. Univ. Mich. Herb. 15:209–217. 1982.

COMMENTS ON THE MIELICHHOFERIOIDEAE OF CENTRAL AMERICA, WITH THE DESCRIPTION OF A NEW SPECIES OF *SYNTHETODONTIUM*

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The Bryaceae are fairly well defined, yet the subfamilial and even the generic limits are difficult to fix. Brotherus (1924) recognized three subfamilies, the Orthodontioideae (with basal membrane none and segments linear), the Bryoideae (with both exostome and endostome well-developed), and the Mielichhoferioideae (with lateral inflorescences and exostome, endostome, or both, reduced or lacking). Andrews (1935, 1940) and Ochi (1959) divided the Bryoideae further into the Pohlioideae and the Bryoideae in a narrow sense. The distinctions between them are not absolute. The Pohlioideae (defined here in a narrow, though informal sense to include *Pohlia, Pseudopohlia,* and *Epipterygium*) have narrow, lanceolate leaves with long, narrow cells and costa ending near the apex. The Bryoideae, generally considered the most primitive subfamily, retain such features as long-tapered, bordered, and trabeculate exostome teeth and well-developed endostomes, with broad, perforate segments and appendiculate cilia rising from a high basal membrane. Of course, many of the Bryoideae show varying degrees of reduction from the well-developed primitive peristome.

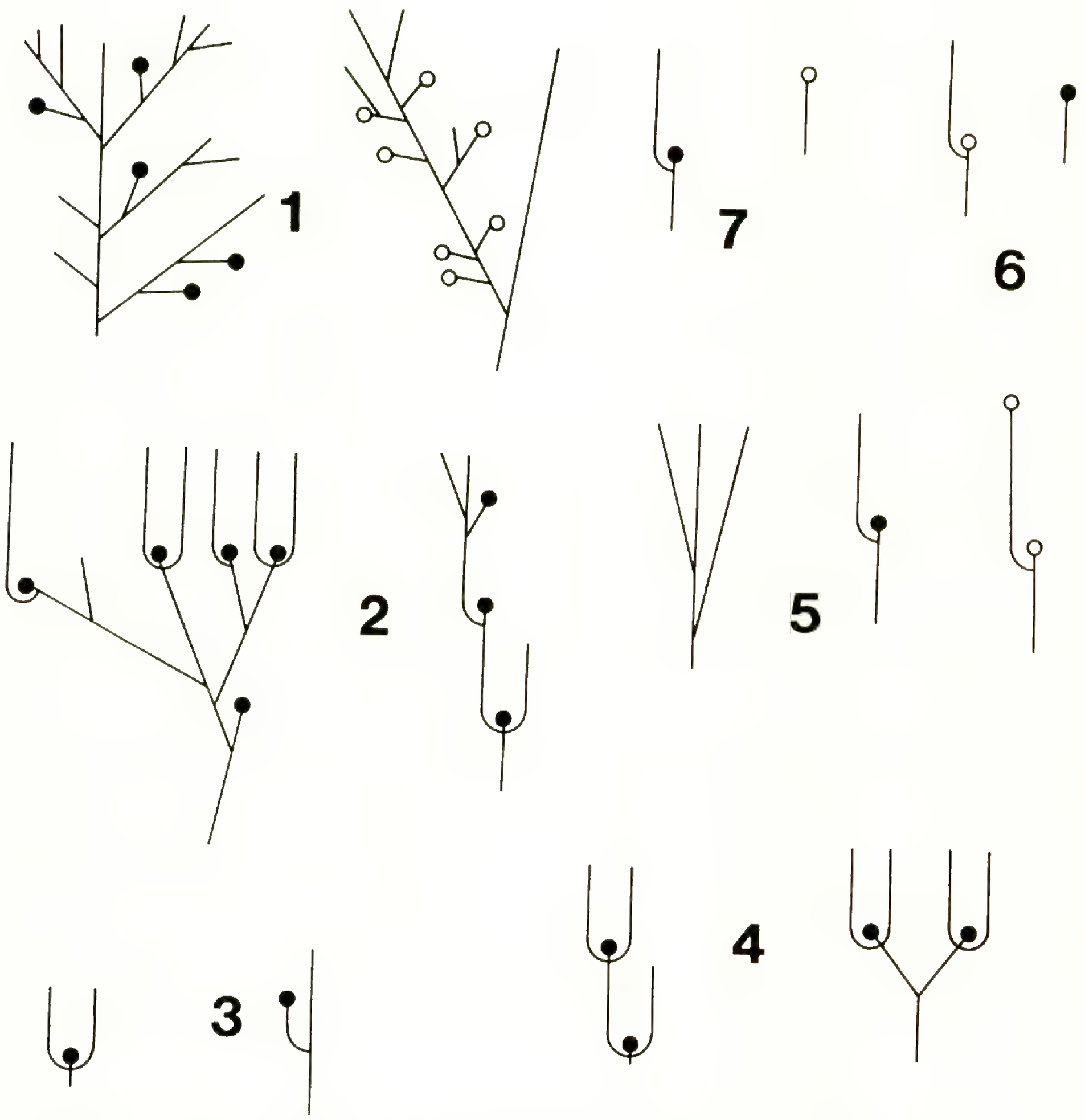
The Pohlioideae share some features of significance with the Mielichhoferioideae (including *Haplodontium, Mielichhoferia,* and *Synthetodontium*). These include lanceolate leaves with long cells and costa not or only shortly excurrent. The Mielichhoferioideae are especially defined in terms of peristome reduction, but there is no single feature that separates that subfamily from the Pohlioideae. *Synthetodontium costaricense,* described here as a new species, could be justifiably placed in *Pohlia* instead.

The criterion most commonly used to separate the Mielichhoferioideae is pleurocarpy. However, inflorescences that appear to be lateral are in some cases terminal on short stems that become overtopped by innovation and displaced to a pseudolateral position. Meusel (1935) suggested that timing determines the degree of lateral displacement. In taxa where the innovation develops early in the season and therefore has time for considerable growth, the inflorescence appears to be borne on a short side branch. But in most species of *Bryum* and *Pohlia* the subfloral innovations develop late and thus have the appearance of secondary branches.

There is considerable diversity of branching patterns in the Mielichhoferioideae. In *M. macrocarpa* (Drumm.) Bruch & Schimp., for example, the plants are freely branched, mainly by innovation. Inflorescences terminate the main stem as well as innovations and fork branches (Fig. 2). In *M. mielichhoferi* (Hook.) Loeske, stems are even more branched, often repeatedly forked (Fig. 1). Male plants tend to branch more freely than female, and perigonia are considerably differentiated as reddish buds at the ends of short lateral branches.

Generally the main stem is identifiable among several finer grades of lateral branches. Innovations occur infrequently, the branches bearing perigonia are scarcely strong enough to give rise to further innovative growth. They are highly specialized reproductive branches with scarcely any vegetative leaves subtending the perigonia. Compared with *M. macrocarpa* and *M. mielichhoferi, M. graciliseta* (Hampe) Mitt. is weakly branched (Fig. 3). Although apparently lateral, the paroicous inflorescences terminate main stems or more rarely lateral branches. The stems fork but not abundantly. *Synthetodontium costaricense* has inflorescences consistently terminal, on short, simple or sparsely forked stems, but appear to be lateral because of multiple innovation (Fig. 4).

In *Pohlia* innovations are common, but forking of the stem is rare. In a few species, such as *P. atropurpurea* (Wahl.) Lindb., the tiny plants are unbranched. *Pohlia drummondii* (C. M.) Andr. normally has innovations below the perigonia but not the perichaetia (Fig. 6); and sterile plants are simple. *Pohlia papillosa* (Jaeg.) Broth., on the other hand, often innovates below female inflorescences, but male plants are simple (Fig. 7). Both male and female plants of *Pohlia wahlenbergii* (Web. & Mohr) Andr. innovate consistently, and unusually robust sterile plants sometimes branch by forking (Fig. 5). Such examples show that the



FIGS. 1–7. Branching patterns. 1. *Mielichhoferia mielichhoferi.* 2. *M. macrocarpa.* 3. *M. graciliseta.* 4. *Synthetodontium costaricense.* 5. *Pohlia wahlenbergii.* 6. *P. drummondii.* 7. *P. papillosa.* (Hollow circles represent perigonia, solid circles perichaetia.)

difference between highly branched Mielichhoferias and simple or sparsely branched Pohlias is a matter of degree, albeit with vastly different extremes.

The Mielichhoferioideae are characterized by peristome reduction, with exostome, endostome or both variously reduced or lacking. Yet Brotherus (1924) listed 13 species of *Mielichhoferia* with double peristomes and both species of *Synthetodontium* have an exostome as well as a fairly well-developed endostome.

It is evident that the primitive Mielichhoferioideae are not entirely distinct from some of the more advanced Pohlioideae. Such continuities are to be expected, of course, if the two families are derived from a common ancestry. We discuss below several taxa of the Mielichhoferioideae with a relatively primitive position.

THE MEXICAN AND CENTRAL AMERICAN MIELICHHOFERIOIDEAE

Synthetodontium has a double, fairly well-developed peristome, with the endostome partly or almost entirely adherent to the exostome. The genus consists of two species: *S. costaricense* Shaw & Crum (described below) and *S. pringlei* Card., known from two collections in Mexico (Jalisco). *Mielichhoferia*, consisting of several species enumerated below, has a more reduced peristome—lacking, single and consisting of endostome only, or double. *Haplodontium* has a reduced, single peristome consisting of exostome only. *Haplodontium argentifolium* (Mitt.) Jaeg. & Sauerb. grows on soil of banks and in rock crevices at altitudes of about 12,500 ft. in Mexico (Distrito Federal and Puebla). It should be noted that *Mielichhoferia* lacks definition. In at least one species of more northern distribution, *M. mielichhoferi* (Hook.) Loeske, the single peristome is actually exostome. Since *M. mielichhoferi* provides the type of the genus, this observation carries significant nomenclatural implications. However, a much needed re-evaluation of the subfamily might lead to combining *Mielichhoferia* and *Haplodontium* to allow for varying kinds and degrees of peristomial reduction. We thus make no transfers pending results from studies in progress.

KEY TO THE SPECIES OF *MIELICHHOFERIA* IN MEXICO (AND ELSEWHERE IN CENTRAL AMERICA)

1. Peristome lacking (or sometimes present but very poorly developed and shed with the operculum). 3. *M. schiedeana*
1. Peristome present.
   2. Peristome single.
      3. Endostome segments papillose, irregular-margined; leaves distinctly serrulate. 2. *M. serrata*
      3. Endostome segments smooth, not particularly irregular-margined. 1. *M. campylocarpa*
   2. Peristome double.
      4. Capsules broadly pyriform; exostome teeth not or scarcely exceeding the annulus. 4. *M. landii*
      4. Capsules cylindric; exostome teeth ½–⅔ the length of the exostome. 5. *M. graciliseta*

1. **M. campylocarpa** (Hook. & W.–Arn. *ex* Hook.) Mitt. On turfy and rocky soil at 9750–15,000 ft. alt. on Mexico's high volcanic peaks; Jalisco (Nevado de Colima), México (Nevado de Toluca), Puebla (Ixtaccíhuatl), and Veracruz (Orizaba; also between Perote and El Cofre).—Mexico and Guatemala; Ecuador, Bolivia, and Peru; recently reported from a wide range in South Africa, Rhodesia, Kerguelen, Australia, New Zealand, Marion Island, and Hawaii.

2. **M. serata** Card. & Herz. *ex* Card. On rocky soil, 9200–13,000 ft. alt.; México (Nevado de Toluca), Puebla (La Venta), and Veracruz (Orizaba).—Endemic.

3. **M. schiedeana** C. M. On soil among rocks and in crevices at 10,500–15,000 ft. on Mexico's high volcanoes (Toluca and nearby Zinantecatl, Popocatepetl, Ixtaccíhuatl, and Orizaba).—Endemic.

4. **M. landii** Card. On soil at 7000–11,000 ft. alt., in pine zones or in the transition to open terrain; Distrito Federal, Hidalgo, México, Oaxaca, and Puebla.—Endemic.

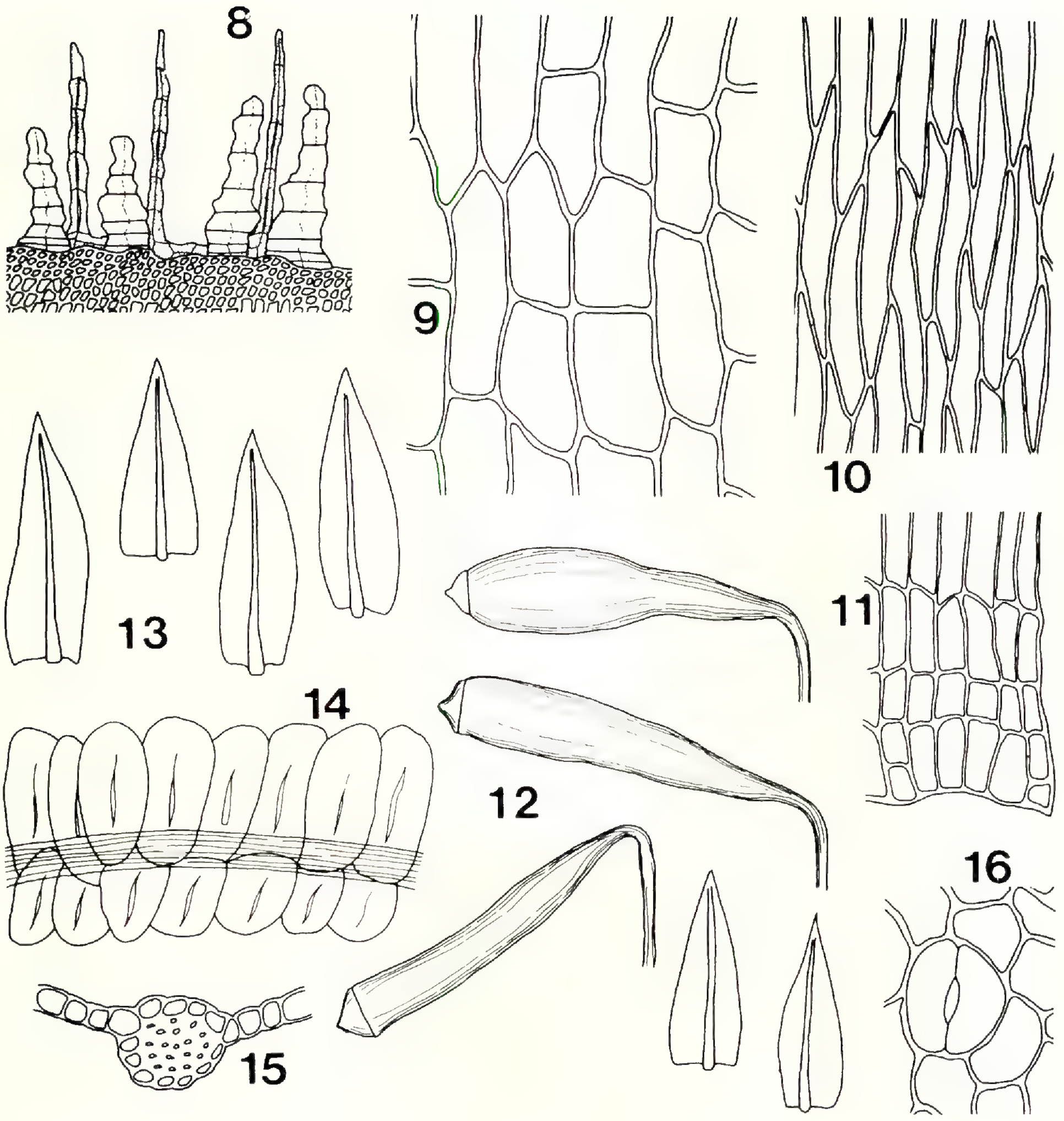
5. **Mielichhoferia graciliseta** (Hampe) Mitt., Jour. Linn. Soc. London, Bot. 12: 324. 1869. *Leptochlaena graciliseta* Hampe, Linnaea 32: 130. 1863.

Small or medium-sized, whitish or reddish plants. Stems 5–10 mm high, branched by innovation, sometimes forked. Rhizoids restricted to the base of the stem, orange, papillose. Leaves of innovations erect to erect-spreading, 0.8–1.2 mm long and 0.4–0.6 mm wide, lanceolate; margins plane, serrate near the apex, serrulate to the midleaf or more; costa ending a few cells below the apex; cells linear-rhomboidal and ± vermicular, thin-walled, 45–75(130) × 7–10 μm, not differentiated at the margins. Paroicous; inflorescences terminal on main stems or short to elongate side branches, bulbiform; perichaetial bracts concave, broadly lanceolate, reddish. Setae 8–13 mm long; capsules inclined at 45–100°, 1.5–3 mm long, narrowly pyriform; annulus broad (of 2–3 rows of cells); operculum convex to conic, blunt or apiculate; exothecial cells rectangular, 50–75 × 20–35 μm, with evenly thickened, ± sinuose walls; stomata superficial, with guard cells 40–50 μm long; exostome teeth irregularly lanceolate, blunt, ⅓–¾ as long as the endostome, varying from 150–280 μm long, sometimes on the same capsule, hyaline or very pale yellow, smooth or finely roughened, not or scarcely bordered, moderately trabeculate, with trabeculae irregularly projecting at the sides; endostome hyaline or pale-yellow, consisting of a distinct, though low basal membrane (scarcely exceeding the annulus), linear segments, scarcely keeled or perforate, often joined at the tips, papillose in the upper half, nearly smooth below, and cilia lacking. Spore 15–19 μm, very finely roughened. Figs. 8–16.

On soil or rock ledges and in crevices (at least sometimes on limestone), sometimes on banks of streams, at 2900–3600 m. alt.; Mexico (Oaxaca, Ixtlán, *Hermann 26912a*; Sierra Juárez, *Richards, Sharp & Sharp 2769, Sharp 98506*); Colombia, Venezuela, and (as *M. castanea* Herz.) probably Bolivia). Bartram (1951) erroneously reported *M. graciliseta* from Costa Rica. The specimen is recorded below as the type of *Synthetodontium costaricense*.

The double peristome, with the endostome considerable longer than the exostome, is the most significant feature of this species, not previously recorded from Mexico. Hampe described the species in the genus *Leptochlaena* which he distinguished from *Mielichhoferia* on the basis of the double peristome. The generic name is, however, a later homonym of *Leptochlaena* Spreng. Mitten (1869) used the name at the sectional level, where it is legal. Brotherus (1924) established the subgenus *Mielichhoferiopsis* for double-peristome species of *Mielichhoferia*. Use of the suffix *-opsis* is, however, contrary to article 2 of the international code of botanical nomenclature.

Brotherus' treatment (1924, pp. 353–354) is not entirely trustworthy. For example, *M. lindigii* Hampe is characterized as having a double peristome. Mitten (1869) placed that species in a group with "peristomium simplex internum." Hampe did not clearly indicate whether the peristome is single or double, but his statement that *Leptochlaena graciliseta* has the stature of a *Mielichhoferia* but a double peristome suggests that he would have placed *M. lindigii* in *Mielichhoferia* because of its single peristome. A more confusing situation is met with in Brotherus' treatment of *M. graciliseta*. He illustrated it (p. 354) as having an endostome about twice the length of the exostome, but his key characterizes the peristome as double with both exostome and endostome similar in length or the endostome shorter. A specimen in Hampe's herbarium with data matching that of the type (Bogotá, La Penna, 2800 m, *Lindig 2014*) has teeth about half as



FIGS. 8–16. *Mielichhoferia graciliseta*. 8. Peristome, ×115. 9. Exothecial cells, ×490. 10. Upper leaf cells, ×490. 11. Alar cells, ×490. 12. Capsules, ×11. 13. Leaves, ×30. 14. Annulus, ×490. 15. Costa in section, ×490. 16. Stoma, ×490.

long as the segments, just as in Brotherus' illustration. Mitten cited, in addition to that collection one also from the Andes Bogotenses, *Wier* 181, represented at BM and in triplicate at NY. One of the specimens at NY is accompanied by Mitten's sketches showing endostome and exostome of equal length. Examination of the material, however, shows that Mitten was in error as the peristome is exactly as Brotherus illustrated it. It may be that Brotherus' confused text was influenced by Mitten's sketches.

The peristome of *M. castanea* Broth. *ex* Herz., as illustrated by Herzog (1916), closely matches that of *M. graciliseta*. In both species the segments of the endostome are commonly joined at the tips. Very likely the names are synonymous.

Pohlia pseudobarbula (Thér.) Shaw (of Mexico) has a peristome scarcely more complete than that of *M. graciliseta*. The exostome teeth, though longer than the endostome, are blunt, hyaline and nearly smooth below, and scarcely trabeculate or bordered, as in *M. graciliseta*. It is tempting to think of the double-peristome

Mielichhoferia as an advanced *Pohlia* (judged in terms of peristome reduction in more advanced members of the genus *Pohlia*). Herzog (1926), in fact, suggested such a relationship between *Mielichhoferia* and *Pohlia*.

The only other Mexican *Mielichhoferia* with a double peristome is *M. landii*. It has the peristome even more reduced. The exostome is very short, no more than 100 μm high and usually completely hidden by the annulus.

Mielichhoferia macrocarpa (Hook.) Bruch & Schimp. has been reported from Mexico on the basis of a sterile collection made by Hahn on the Nevado de Toluca. The plants do not compare at all well with *M. macrocarpa* as the leaf margins are less clearly recurved and more strongly toothed, and the leaf cells are shorter and thicker-walled.

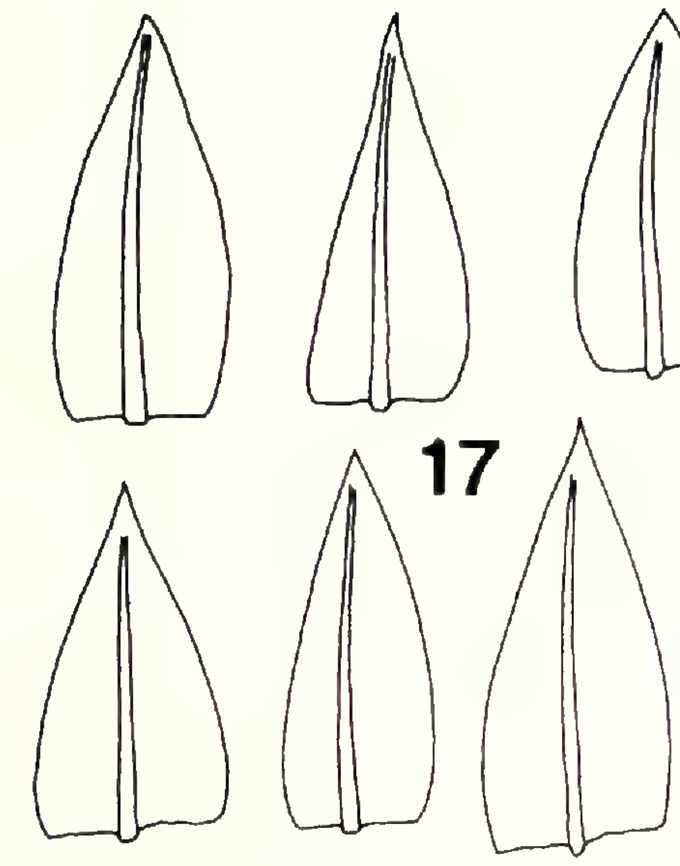
Because of a well-developed, almost *Pohlia*-like peristome the following new species of *Synthetodontium* is particularly significant in indicating a phylogenetic trend from the Pohlioideae into the Mielichhoferioideae:

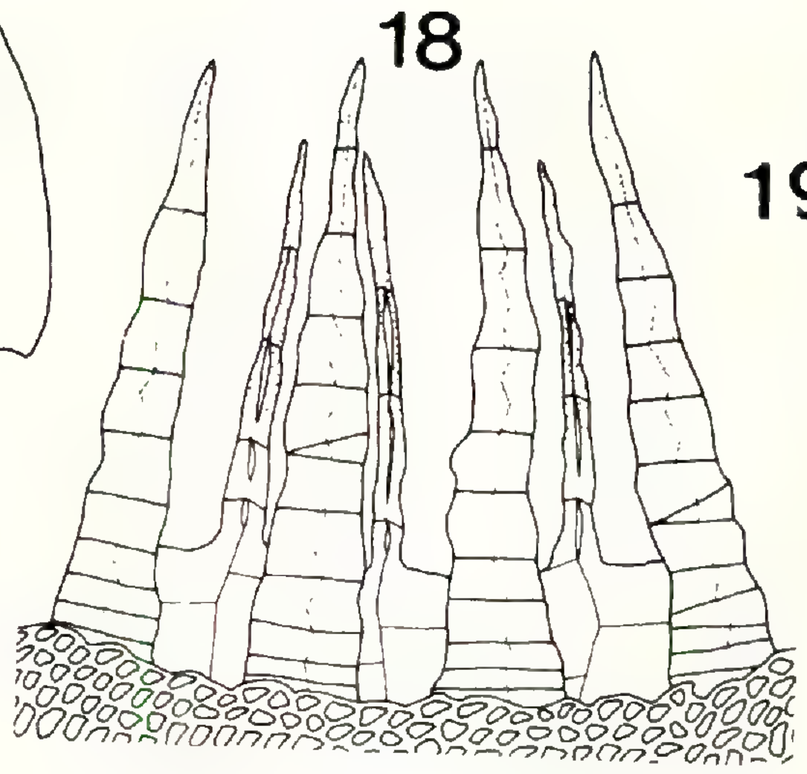
Synthetodontium costaricense Shaw & Crum, sp. nov.

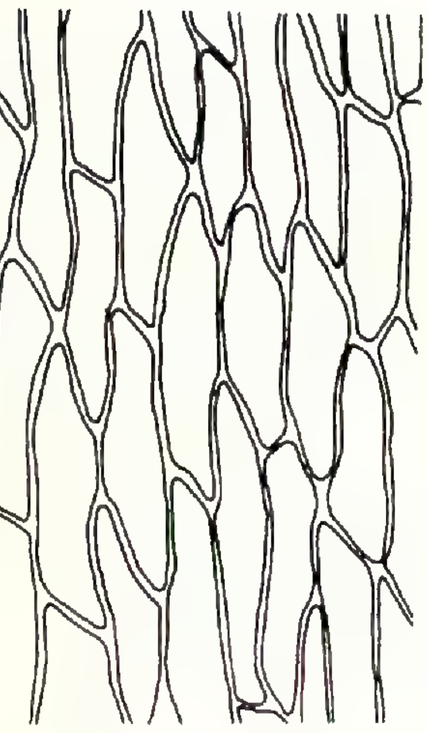
Plantae graciles, 5–9 mm altae, rubrae vel aureae, ± nitidae, caulibus innovando ramosis, fructificationibus simulate lateralibus. Folia 0.8–1.2 mm longa, lanceolata, acuta, haud vel ± limbata; costa subpercurrens; cellulae rhomboideales. Dioicum. Seta usque ad 10 mm altitudine; capsula ± erecta, anguste pyriformis, 2–3.5 mm longa; annulus latus; operculum convexum; peristomium duplex, exostomii dentes ca 3000 μm longi, lanceolato-acuminati, papillosi, inferne aurantiaci; endostomium membrana basilari ± alta, processibus angustis, carinatis, ± perforatis. Sporae 12–17 μ, laeves vel subtiliter papillosae.

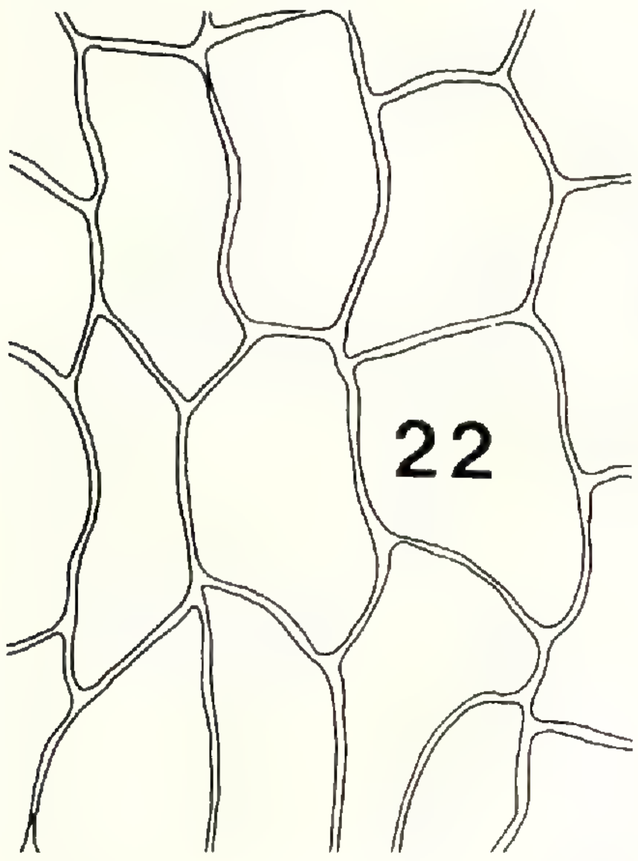
Very small, reddish to golden, ± glossy plants. Stems 5–9 mm high, freely branched by subfloral innovation, occasionally forked, with a poorly developed central strand surrounded by gradually larger, thin-walled cells and 2–4 peripheral layers of abruptly differentiated thick-walled cells. Rhizoids restricted to the base of the stems, orange, densely papillose. Leaves of innovations erect to erect-spreading, ± concave, 0.8–1.2 mm long and 0.3–0.6 mm wide, lanceolate, acute; margins plane or slightly reflexed; costa ending a few cells below the apex; upper cells rhomboidal, varying from 45–75(125) × 9–15 μm, rather thin-walled, undifferentiated at the margins or ± abruptly elongate in 3–5 rows forming a distinct, sometimes yellowish border; basal cells gradually to abruptly enlarged and rectangular, or sometimes scarcely differentiated. Dioicous; perichaetia terminal but appearing to be lateral because of well-developed innovations, perichaetial bracts reddish, concave, lanceolate to broadly triangular, with margins ± recurved; perigonia bulbiform, at the ends of short, inconspicuous stems, sometimes appearing lateral because of innovation, the perigonial bracts erect, concave, ovate, shortly and broadly acute; paraphyses abundant, filiform, pink to orange. Setae up to about 10 mm; capsules erect or nearly so, 2–3.5 mm long, narrowly pyriform, with the neck about as long as the urn; annulus broad consisting of 2–3 rows of cells and about 100 μm high; operculum convex, blunt; exothecial cells 45–65 × 12–26 μm, rectangular, with straight, evenly thickened walls; stomata superficial or slightly sunken, the guard cells ca. 40 μm long; exostome teeth ca. 300 μm long, lanceolate, slenderly acuminate, orange and very finely papillose below, gradually becoming pale to hyaline and finely papillose, above, strongly bordered, trabeculate; endostome yellow, sometimes ± adherent to the exostome, with a basal membrane about ⅓ the length of the exostome, narrow but keeled and ± perforate segments, smooth or finely papillose below, and subhyaline above, cilia none. Spores 12–17 μm, smooth or finely roughened. Figs. 17–26.

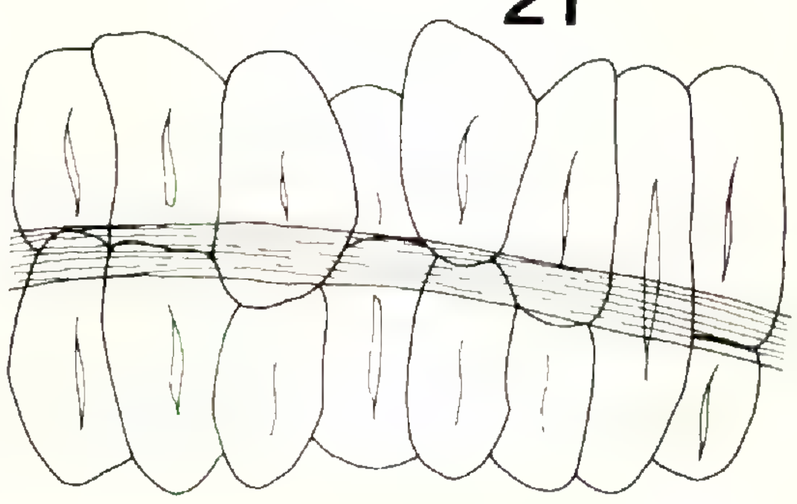
Cloud forest, ca. 10,000 ft., Roberts' Farm, S. slope of Mt. Irazú, prov. Cartago, Costa Rica, *Ruth D. Svihla* (holotype, FH, a *Mielichhoferia graciliseta*).

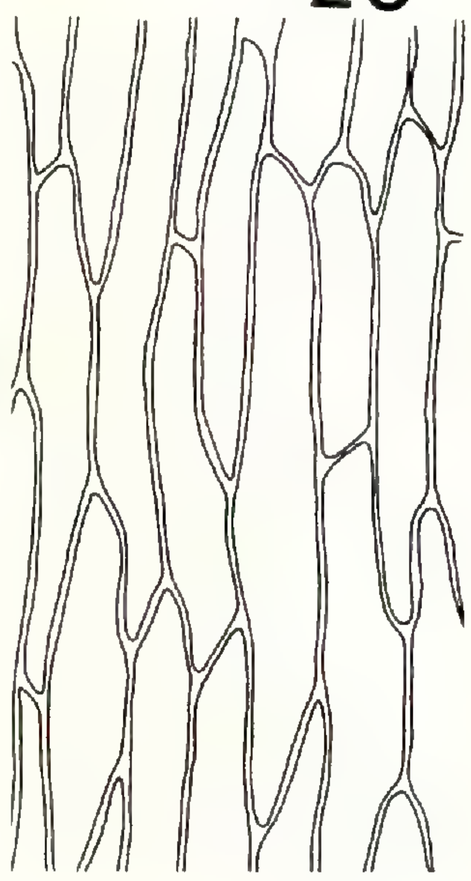


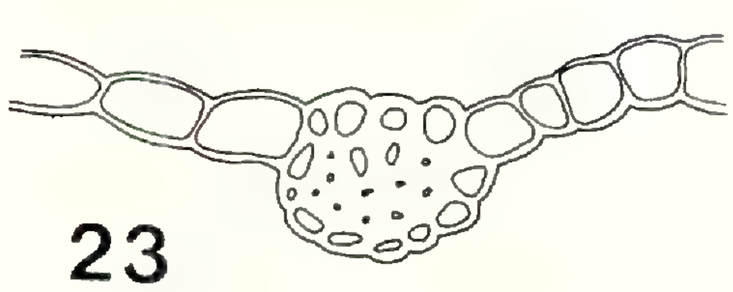


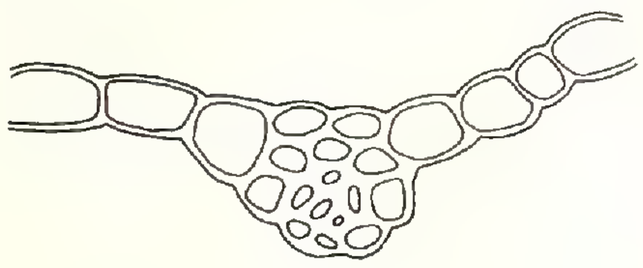


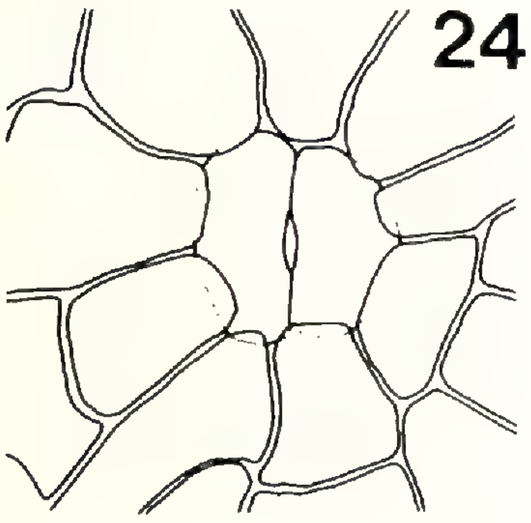


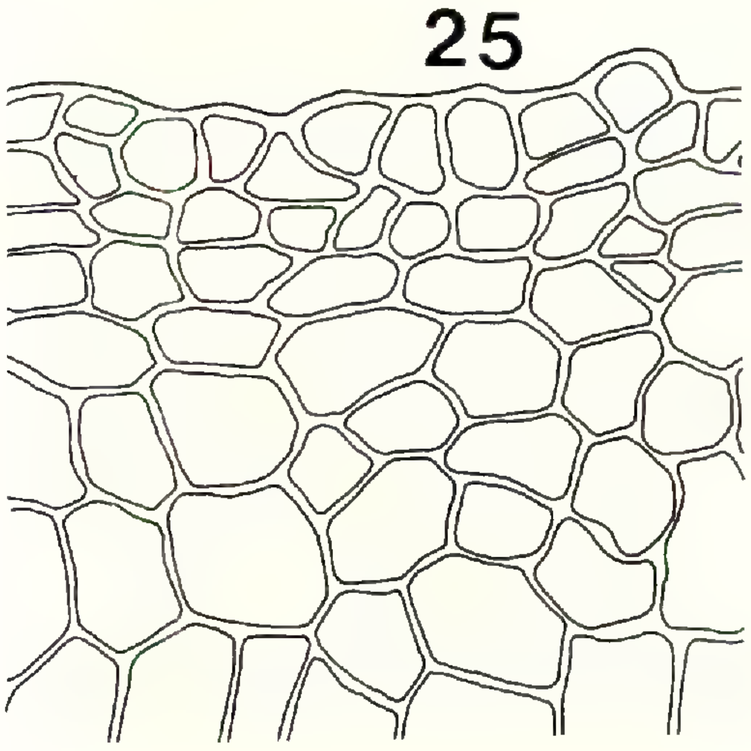


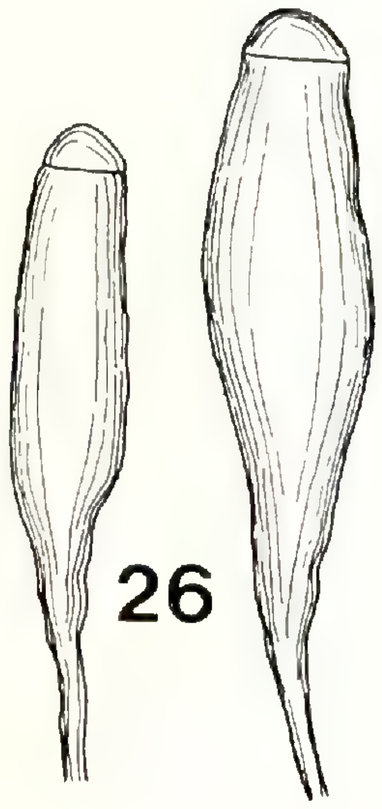












FIGS. 17–26. *Synthetodontium costaricense.* 17. Leaves, ×30. 18. Peristome, ×115. 19, 20. Upper leaf cells, ×490. 21. Annulus, ×490. 22. Exothecial cells, ×490. 23. Costa sections, ×490. 24. Stoma, ×490. 25. Exothecial cells near the capsule mouth, ×490. 26. Capsules, ×11.

The genus is characterized by a double peristome with perforate segments arising from a basal membrane about one-third the length of the exostome which consists of long-tapered teeth, orange below, hyaline above. The only other species of the genus, *S. pringlei* Card., is known from two localities in the state of Jalisco, Mexico. It has endostome segments adherent to the exostome teeth giving a chambered appearance rather like that of *Bryum algovicum* Sendtn.

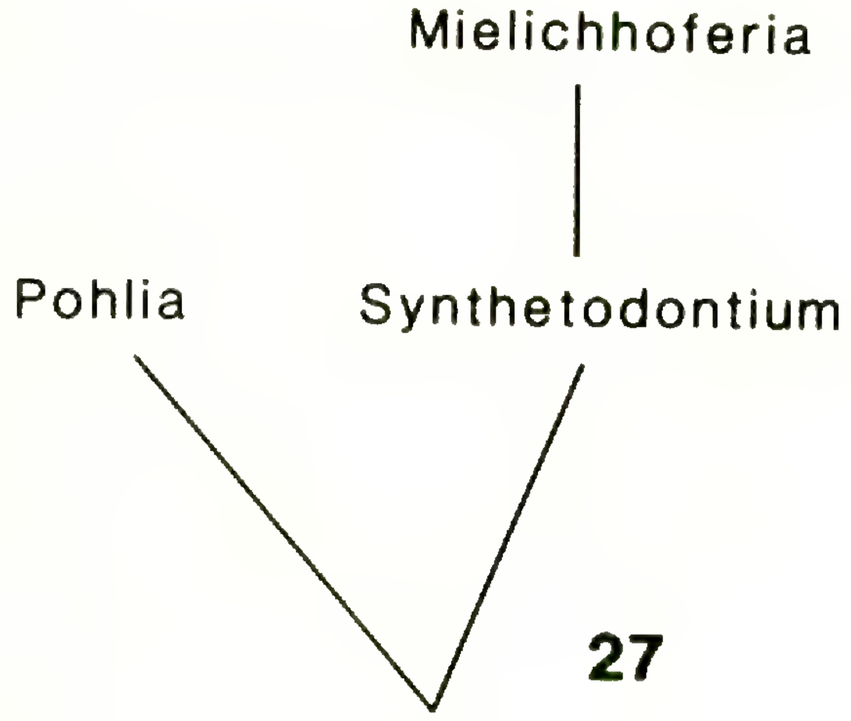
ex C. M. According to Cardot each segment becomes split into two parts each adhering to an adjacent tooth and appearing to form a narrow, sinuose border. Actually, as we have seen them and as Georg Roth showed them in manuscript drawing, they are very delicate and irregular in outline but fully adherent and not bifid.

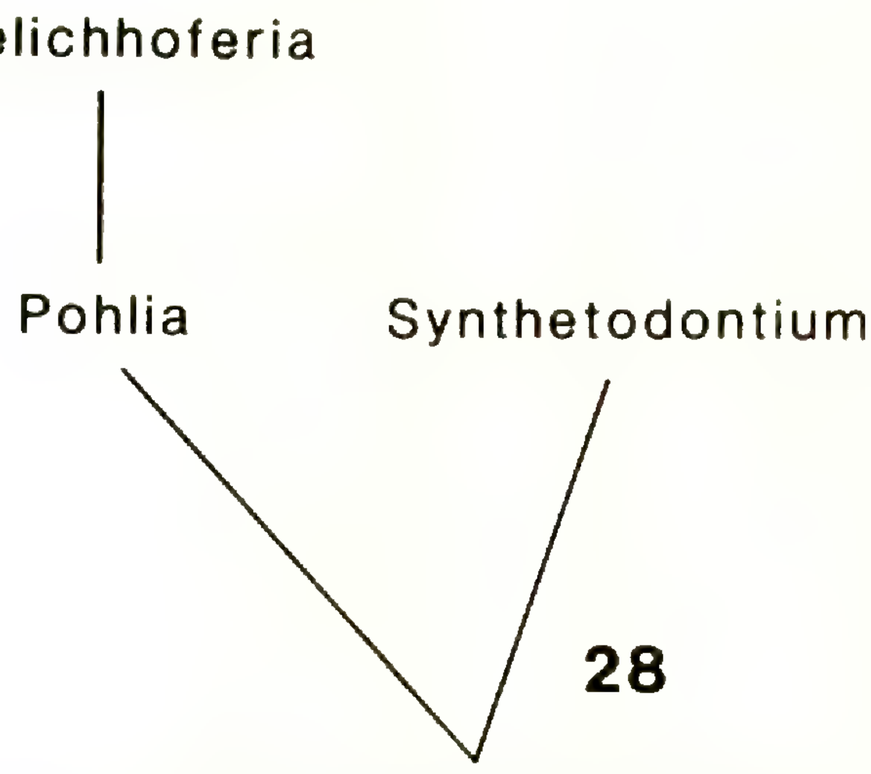
In *S. costaricense* the exostome and endostome are mostly free (though sometimes adherent below). It has red-brown, acute leaves and spores 12–17 μm. *Synthetodontium pringlei* has pale-green, broadly acute to obtuse leaves and spores 25–30 μm. The cells at the leaf margins are sometimes differentiated as a border in *S. costaricense*; the border may vary from fairly distinct and often yellowish to none at all even on the same plants.

The genus *Synthetodontium* has some phylogenetic significance since its peristome, being relatively well developed, is decidedly primitive among the more reduced peristomes generally representative of the Mielichhoferioideae. The exostome teeth are regular in development and long-tapered, showing scarcely any resemblance to those of the double-peristome Mielichhoferias such as *M. graciliseta*. There is, in fact, little to distinguish the exostome from that of such an otherwise dissimilar species as *Bryum algovicum*. Furthermore, the endostome segments are keeled and more or less perforate, unlike those of other Mielichhoferioideae, though like those commonly found in *Pohlia*. We must admit that with no prior knowledge of *Synthetodontium* as a genus we might have described *S. costaricense* as a *Pohlia*, though perhaps in its own subgenus. In any case, *Synthetodontium* may be close to the ancestral origins of the Mielichhoferioideae and the Pohlioideae.

The rather well-differentiated bud-like inflorescences seem to link *Synthetodontium* to the Mielichhoferioideae, at least as they are now constituted. However, such a linkage presents a dilemma. Both species of *Synthetodontium* and the double-peristome Mielichhoferias suggest relationships to *Pohlia*, but to unrelated taxa. *Synthetodontium pringlei* Card. and *S. costaricense* have exostome teeth resembling those of primitive Pohlias (or even many species of *Bryum*). *Mielichhoferia graciliseta* (and to a lesser degree *M. landii*), on the other hand, show resemblances to such advanced Pohlias as *P. pseudobarbula*.

Either the Mielichhoferioideae are polyphyletic, with only distant phylogenetic linkage between *Mielichhoferia* and *Synthetodontium*, or there is evidence for convergence, by one or the other genus, toward *Pohlia*. These alternatives are shown in figures 27–28: Figure 28 implies that apparently lateral bud-like inflorescences evolved independently, with *Mielichhoferia* evolving from the ancestors of present-day Pohlias with similar peristomes. Figure 27 implicates a





FIGS. 27–28. Alternative hypotheses of phylogenetic relationships of *Pohlia*, *Synthetodontium*, and *Mielichhoferia*.

common ancestor of *Pohlia* and *Synthetodontium* with long-tapered exostome teeth and well-developed endostomes. The similarity in the exostomes of such species as *Mielichhoferia graciliseta* and *Pohlia pseudobarbula* seems due to convergence.

It may be significant that both *Synthetodontium* and *Mielichhoferia graciliseta* (at least) have anatomically similar costae. In *Pohlia* there are usually median guide cells and stereids moderately differentiated or none. In the Mielichhoferioideae examined, stereids fill most of the costa, and guide cells are absent.

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POHLIA HEDW. (MUSCI) IN NORTH AND CENTRAL AMERICA AND THE WEST INDIES

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Within the Bryaceae, basic features defining *Pohlia* are lanceolate, often serrate leaves, costae ending before or in the apex, and long, generally narrow cells. The peristome is double and the endostome is well-developed although cilia, when present, generally lack appendicula. Groups of taxa within the genus are more or less uniform with respect to such attributes as exostome and endostome form and ornamentation, exothecial cell shape, the presence or absence of annuli and the position of stomates relative to their guard cells. Within such groups, species differ mainly with respect to gametophytic details. Axillary gemmae have evolved at least twice in unrelated lines. Rhizoidal tubers are present in *P. lescuriana*, *P. pacifica* and *P. integra*, and are of some use in characterizing these species.

The group of species segregated by some as the genus *Mniobryum* are included here in *Pohlia*, although it is fully acknowledged that *Mniobryum* constitutes a distinctive assemblage. The presence of such species as *P. lescuriana*, which is a *Pohlia* by any definition but approaches the *Mniobryum* group in several significant respects, makes including the latter as an infra-generic taxon in *Pohlia* at least defensible. Crum and Anderson (1981), following Andrews (1935), placed *Bryum apiculatum* Schwaegr. (= *P. cruegeri* Hampe *ex* C. Müll.) in *Pohlia*. However, I agree with Ochi (e.g. 1981) that it is more at home in *Bryum*. It is the long cells that might indicate a relationship to *Pohlia*, but this trait is to be found rather frequently elsewhere in *Bryum*. In addition, the costa is shortly excurrent, and the leaf margins are entire (or vaguely serrulate), features uncommon in *Pohlia*. Although appendiculate cilia are found in a few *Pohlia* species, they are uncommon, and their presence in *B. apiculatum* casts further doubt on a closer relationship to *Pohlia* than to *Bryum*. Finally, the lowland circumtropical distribution of *B. apiculatum* would be unique in *Pohlia*, though not rare in *Bryum*. *Pohlia peracuminata* Bartr. from Guatemala is a similar case where generic placement is uncertain, but according to Ochi (*in litt.* 1981) it can be referred to *Bryum microchaeton* Hampe.

I also follow Ochi in interpreting *Anomobryum* as more allied to *Bryum* than *Pohlia*, although generic status seems justified. The long-narrow cells, which are not even characteristic of all *Anomobryum* species, is the only feature that relates *Anomobryum* to *Pohlia*.

With about 110 species, *Pohlia* is represented on every continent. The circumboreal taxa are by far the best understood, and of the thirty-two Pohlias in North America north of Mexico, twenty-five occur on at least one other northern continent. There have been no revisions of tropical or Southern Hemisphere species.

Many of the American *Pohlia* species are rare throughout their range and the genus is poorly represented in temperate eastern North America. *Pohlia melanodon* and *P. lescuriana* are restricted to eastern North America and are fairly

widespread, though relatively uncommon (*P. lescuriana* is also known from two localities in Alaska). *Pohlia wahlenbergii* and *P. nutans* are common in the northeastern states and extend southward to a considerable extent. Otherwise, species reaching Tennessee and North Carolina do so by following the Appalachian mountain chain. These include *P. cruda, P. elongata,* and *P. longicollis. Pohlia annotina* is fairly widespread in eastern North America, in the mountains and elsewhere.

In the Rocky Mountains and westward, *Pohlia* is one of the most diversified of moss genera. Collecting on the slopes of Mt. Rainier (Washington) for example, can yield up to eight species in a day. Relatively moist areas with acidic soils in the mountains of southern British Columbia are also uncommonly diverse in *Pohlia* species. Several species extend southward in the Rockies to Colorado, but only *P. elongata, P. nutans, P. wahlenbergii* and *P. tundrae* are confirmed in Arizona and (or) New Mexico.

Of the North American species, *P. elongata, P. cruda, P. nutans* and *P. wahlenbergii* reach Mexico, but only *P. elongata* is common there. Other species of Mexico and Central America are either endemic, for example, *P. integra, P. oerstediana* and *P. pseudo-barbula*, or have phytogeographic affinities with Andean plants. The latter includes *P. richardsii* and *P. polycarpa.*

Of the *Pohlia* taxa occurring north of Mexico, six (19%) are endemic. Three of these are found in the Pacific coastal region near or at sea level (*P. longibracteata, P. columbica* and *P. pacifica*), whereas the other three are alpine-high montane in the Cascade and (or) Rocky Mountains. Endemism in Mexico and Central America is more difficult to evaluate since collecting there has been relatively scarce. *Pohlia integra* and *P. pseudo-barbula* are confined to mountains near Mexico City, and *P. oerstediana* extends from central Mexico to Costa Rica. There are no West Indian *Pohlia* endemics and only *P. elongata, P. wahlenbergii, P. richardsii* and *P. papillosa* are known from the islands.

As a whole, *Pohlia* covers a significant diversity of habitats. Most taxa occur on soil, although the substrates of particular species are usually well-defined in terms of pH, texture, organic matter content, and the levels of various ions. The *Mniobryum* group (species 29–36) is found almost exclusively on soils of high pH, 6.5 or above, and low organic content (less than 2.5%). Of those species only *P. longibracteata* occurs frequently on more acidic soil. Species 14–17, including the group of weedy propaguliferous species, also prefer soil with relatively low levels of organic matter (3.5% or less), but they usually occur on mildly acidic soil. The remaining species are almost entirely restricted to acidic soils (pH 4–6).

By far the most common habitat in which to find Pohlias are roadbanks and other disturbed sites. Some such species as *P. annotina* are rarely collected in undisturbed habitats, although most other, less weedy species are found also on streambanks or in soil-filled crevices. Several species reach the alpine zone, and *P. crudoides, P. longicollis* and *P. andrewsii* are characteristic of crevices among siliceous rocks in tundra. Most other species, when they occur in the alpine zone, grow in more exposed sites. *Pohlia obtusifolia* and *P. bolanderi* var. *seriata* prefer exceptionally lush snowmelt areas. *Pohlia sphagnicola* is unique in being restricted to *Sphagnum* hummocks lacking mineral soil.

The main purpose of this paper is to provide an aid in identification. The infra-generic evolution and classification of *Pohlia* will be dealt with elsewhere, and the genus is left undivided here. However, the arrangement of species is intended to represent relationships, insofar as a linear sequence can. Species 1–13 have long-rectangular, nonsinuose exothecial cells, whereas in species 14–35 they are short-rectangular to isodiametric, usually with strongly sinuose walls. Species 10–13 have whitish exostome teeth densely covered with papillae (less so in *P. pseudo-barbula*) and lack cilia altogether. I have dispensed with tradition in, for example, placing *P. elongata* next to *P. nutans* rather than with other species

having narrowly split endostome segments. It is open to question whether endostome simplification has occurred only once in those species, and the present arrangement is intended as noncommital, reflecting gametophytic as well as sporophytic similarity. Of the species with sinuose exothecial cells, 14–27 have annuli, while they are lacking in 28–34. In species with sinuose exothecial cells, they become nearly straight when thoroughly moistened. Axillary gemmae characterize species 11–13 and 17–26.

Many problems relating to nomenclature and typification are not discussed for the sake of brevity. The location of lectotypes are indicated, and further details on specimens are available from the author. The problem of *in* versus *ex* in some author citations was not resolved completely. In such cases as *Webera columbica* Kindb. *in* Kindb. & Macoun, the *in* allows the name to be typified from Kindberg's herbarium, as most bryologists would agree it should. It should be admitted that in such other cases as *P. longibracteata* Broth. *in* Roell., the choice of *in* is to facilitate typification since there is little evidence from the original publication to make a decision as to whether *in* or *ex* is more appropriate.

A revision of species 18–26 was published previously (Shaw, 1981a), and only brief descriptions and illustrations are given here. *Pohlia beringiensis* (17) is described for the first time. Although sterile, similarities in gemmae structure relate it to *P. drummondii* (18). Gemmae similar to those of species 17–26 are produced by *P. papillosa*, *P. richardsii* and *P. pseudo-barbula*, but other characters, especially sporophytic, indicate that the two groups are only distantly related.

Keys are provided for both fertile and non-fruiting plants, although identification may require at least a determination of sexuality. The key to non-fruiting plants is offered somewhat apologetically since gametophytic distinctions, though often reliable, are difficult to define and consequently to use.

Except where noted, geographic distributions given are based on specimens examined. I did not attempt to exhaustively document the local distributions of such common species as *P. wahlenbergii*, *P. cruda* and *P. nutans*, and so maps should be considered synoptic. Greenland distributions shown on maps are given incidentally.

Pohlia Hedw., Spec. Musc. 171. 1801.

Webera Hedw., Spec. Musc. 168. 1801 (hom. illeg., non Webera Schreb.).

Lamprophyllum Lindb., Oefv. K. Vet. Ak. Foerh. 20: 12. 1863 (*hom. illeg., non Lamprophyllum* Miers.).

Mniobryum Schimp. *ex* Limpr., Laubm. Deutsch. 2: 272. 1892.

Small to robust, glossy or dull plants generally forming populations of restricted size, occasionally mixed with other mosses. Stems erect, short to very long, simple or branching at the base or less commonly above when sterile, simple or often innovating when bearing gametangia, in transverse section round to pentagonal, with a ± distinct central cylinder of small, thin-walled cells, 4–7 rows of gradually larger thin- to thick-walled cells and 1–4 (–6) rows of small, often pigmented thick-walled peripheral cells. Rhizoids pale orange-red to brown, papillose, sometimes bearing tubers. Leaves little altered when dry, symmetric or ± asymmetric, lanceolate to ovate-lanceolate (linear in the S. Hemisphere *P. tenuifolia*), acute or rarely rounded at the apex, generally ± decurent; margins plane to recurved (especially the perichaetial bracts), serrate to serrulate or rarely entire near the apices, entire to serrulate below; costa single, ending above mid-leaf to percurrent, rarely shortly excurrent, occasionally abruptly widened below, in transverse section rounded to plane on the ventral (upper) surface, ± strongly convex on the dorsal surface, with 2–4 median guide cells, a ± well-developed dorsal stereid band, sometimes a few ventral stereids, and 1 row of enlarged firm-walled cells on the dorsal and

ventral surfaces; upper cells hexagonal to linear, sometimes large and lax, smooth, with thin to thickened walls, lower cells hexagonal, often quadrate across the insertion, marginal cells undifferentiated or in some species longer and narrower than the median. Propagula sometimes present in the upper leaf axils, arising singly or in clusters of 3-many, consisting of a multicellular body and (0–)1–4 apical or subapical leaf primordia. Dioicous, paroicous or rarely autoicous; perichaetia terminating short to elongate main stems, the bracts scarcely to strongly differentiated, with recurved margins; perigonia terminal on main stems or sometimes innovations, the bracts shortly acute to longly acuminate from an ovate, concave, ± red-brown base, erect to spreading or sometimes squarrose from the erect base; paraphyses filiform, orange to pink. Sporophytes rare to common; setae erect, in transverse section similar to the stem but with a more strongly developed central cylinder; capsules 1 or rarely more per inflorescence, inclined to erect, ovate-pyriform to linear-cylindric, sometimes urceolate, with a well-developed neck, very small to large; exothecial cells isodiametric to elongate and rectangular, sometimes collenchymatous, the walls straight to sinuose, smaller, thicker-walled and less sinuose near the rim, isodiametric with thin to firm, straight walls in the neck, gradually more elongate with thickened, straight walls just above the seta; stomata abundant in the neck, with 2 guard cells, superficial, sunken, or deeply immersed; annuli well developed to absent, (1–)2–3 rows of cells, revoluble or separating irregularly; opercula conic to convex, acute, apiculate, umbonate or rarely rostrate; calyptrae cucullate, smooth; peristome, double; exostome teeth 16, lanceolate, acute to acuminate and 300–550 μm long, or rarely ± blunt and about 150–300 μm long, strongly to obscurely bordered, with dorsal plates wider but ventral plates thicker; endostome well-developed or incomplete, hyaline or sometimes yellow; basal membrane low to high; segments generally elongate and keeled, broadly to narrowly (or not at all) perforate; cilia long and nodulose to short or absent. Spores very finely to coarsely roughened.

KEY TO STERILE PLANTS

1. Plants bearing axillary gemmae.
   2. Gemmae arising singly in the leaf axils.
      3. Plants conspicuously whitish; leaves erect. 17. *P. beringiensis*
      3. Plants green, reddish or black; leaves erect or spreading.
         4. Gemmae translucent orange-red; leaf primordia the same color as the body. 13. *P. pseudo-barbula*
         4. Gemmae opaque, reddish to orange or green, sometimes black; primordia green or pale.
            5. Gemmae cylindrical to oblong, reddish when moist; leaf primordia green and conspicuous, scattered on the body and at the apex. 18. *P. drummondii*
            5. Gemmae elliptic to ovoid, orange when moist (often black when dried); primordia pale, stiffly triangular, mostly restricted to the apex. 19. *P. filum*
   2. Gemmae arising in clusters.
      6. Gemmae spheric to short-oblong, hardly longer than wide.
         7. Primordia of gemmae triangular-laminate, forming a dome over the apex. 22. *P. bulbifera*
         7. Primordia of some or all gemmae peglike (just 1–2 cells broad at the base), erect or ± incurved over the apex.
            8. Gemmae yellow or brown, isodiametric or nearly so. 26. *P. camptotrachela*
            8. Gemmae orange or red, a little longer than wide.
               9. Plants glossy (arctic). 23. *P. andrewsii*
               9. Plants dull (tropical). 12. *P. richardsii*
      6. Gemmae oblong, obconic or ± elongate and vermicular.
         10. Gemmae small (about 110 μm) and orange-red, with the primordia peglike and incurved. go to 8
         10. Gemmae larger, oblong, obconic or linear-vermicular.
            11. Plants glossy.

12. Leaf primordia laminate, at least 3–4 cells broad at the base.
    13. Gemmae oblong or obconic. 20. *P. andalusica*
    13. Gemmae linear-cylindrical. 21. *P. tundrae*
12. Leaf primordia peglike, 1–2 cells broad at the base (gemmae linear-vermicular). 24. *P. proligera*

11. Plants dull.
    14. Gemmae linear-vermicular with one primordium, less commonly oblong with 2–4 primordia (tropical and subtropical). 11. *P. papillosa*
    14. Gemmae oblong or obconic to linear-obconic.
        15. Stems mostly simple; gemmae linear, obconic or oblong, green, yellow, hyaline or orange (temperate and subarctic North America). 25. *P. annotina*
        15. Stems often forking, gemmae broadly oblong or ovoid, reddish-orange (Mexico). 13. *P. pseudo-barbula*

1. Plants without axillary gemmae.
    16. Rhizoidal tubers obviously present.
        17. Plants shiny yellow-green; cells laxly and broadly rhomboidal; tubers red (Mexico). 36. *P. integra*
        17. Plants dull or somewhat glossy green; cells linear rhomboidal, tubers yellow, orange or orange-brown (temperate North America). 28. *P. lescuriana*
    16. Tubers lacking.
        18. Leaf margins strongly recurved.
            19. Stems red, leaves longly lanceolate; cells linear-hexagonal, thin-walled. 10. *P. crudoides*
            19. Stems green, leaves lanceolate; cells rhomboidal, rather thick-walled, sometimes porose. 15. *P. cardotii*
        18. Leaf margins plane (except the perichaetial bracts).
            20. Cells broad, 13 μm or more wide.
                21. Plants dull whitish, in calcareous seepy or wet areas. 29. *P. wahlenbergii*
                21. Plants yellow-green, reddish or blackish, at least below, in calcareous or acidic, usually wet sites.
                    22. Plants often robust, to 1 cm or more high, often blackish below and pale green just near the tips. 9. *P. obtusifolia*
                    22. Plants slender, 3–8 mm high, yellowish or reddish.
                        23. Plants slender, yellowish, somewhat glossy. 30. *P. melanodon*
                        23. Plants tiny, populations rarely consisting of more than a few stems, reddish. 31. *P. atropurpurea*
            20. Cells narrow, 6–10(–12) μm wide.
                24. Cells conspicuously thick-walled.
                    25. Plants dioicous; leaves nearly entire. 1. *P. sphagnicola*
                    25. Plants paroicous; leaves ± serrate near the apex. 2. *P. nutans* or 3. *P. elongata*
                24. Cells with thin to firm walls.
                    26. Plants whitish, with the leaves often erect and seriate.
                        27. Plants slender, to 1 cm high. 32. *P. brevinervis*
                        27. Plants medium size to robust.
                            28. Leaves erect and often seriate, lanceolate. 6a. *P. bolanderi* var. *seriata*
                            28. Leaves ± spreading, not seriate, broadly lanceolate to elliptic. 4. *P. cruda*
                    26. Plants shiny or dull green, the leaves sometimes erect but not whitish.
                        29. Plants paroicous.
                            30. Plants dull or slightly glossy, pale green, 1.5–3.5 cm high (Mexico, Central America). 5. *P. oerstediana*
                            30. Plants, very glossy, green or pale green, 0.5–2.0 mm high.
                                31. Leaves long-laneolate, erect, coarsely serrate near the apex. 7. *P. longicollis*
                                31. Leaves broadly lanceolate, spreading to erect-spreading, serrate or serrulate near the apex. 4. *P. cruda*
                        29. Plants dioicous.
                            32. Leaves widespreading, narrowly lanceolate; perigonial bracts very long-acuminate, to 6 mm long. 35. *P. longibracteata*
                            32. Leaves erect to ± spreading, lanceolate or broadly lanceolate; perigonial bracts shorter, to 3–4 mm.
                                33. Plants robust; leaves broadly acute to rounded, long-decurrent, those low on the stem often pink. 14. *P.ludwigii*

33. Plants slender to medium size; leaves acute, shortly or not at all decurrent, lower leaves green (all leaves ± reddish in *P. columbica*).
    34. Plants high in the mountains or in the north.
        35. Stems red.
            36. Plants slender with erect-appressed leaves. 33. *P. vexans*
            36. Plants medium size with erect-spreading, soft-appearing leaves. 16. *P. erecta*
        35. Stems green, orange or brown.
            37. Plants of South and Central America. 8. *P. polycarpa*
            37. Plants of the western United States and Canada. 6. *P. bolanderi*
    34. Plants at or near sea level.
        38. Plants very glossy light green. 27. *P. pacifica*
        38. Plants dull or slightly glossy, green or reddish.
            39. Plants dull or slightly glossy, green; perigonial bracts erect or erect-spreading. 28. *P. lescuriana*
            39. Plant dull reddish; perigonial bracts wide-spreading. 34. *P. columbica*

KEY TO PLANTS BEARING SPOROPHYTES

1. Exothecial cells plainly bulging.
    2. Gemmae red or orange, shortly oblong to isodiametric; leaf primordia incurved. 12. *P. richardsii*
    2. Gemmae green, yellow, pink or hyaline, linear-vermicular or less commonly oblong; primordia erect, rarely poorly developed and incurved. 11. *P. papillosa*
1. Exothecial cells not bulging.
    3. Annulus absent; exothecial cells little or no longer than wide.
        4. Cells laxly and broadly rhomboidal, 12 μm or more wide.
            5. Plants tiny (2–6 mm), often reddish; stomates superficial or somewhat immersed; cells of perichaetial bracts narrow (6–10 μm). 30. *P. atropurpurea*
            5. Plants small to robust (5–35 mm), yellowish or whitish-green; most stomates deeply immersed; cells or perichaetial leaves broad, 12–20 μm broad.
                6. Plants pale, whitish-green, 1–5 cm high. 28. *P. wahlenbergii*
                6. Plants yellowish glossy-green, 0.5–1.0 cm high. 29. *P. melanodon*
        4. Cells linear-hexagonal, 6–10 μm wide.
            7. Plants robust; leaves wide-spreading; perigonial bracts long-acuminate, to 6 mm long. 34. *P. longibracteata*
            7. Plants slender; leaves erect to erect-spreading; perigonial bracts shorter, to 3–4 mm long.
                8. Stomates superficial or slightly sunken.
                    9. Stems elongate, to 1 cm or more high; leaves erect, whitish; cells of all leaves linear, 6–9 μm wide. 31. *P. brevinervis*
                    9. Stems short, 2–6 mm; leaves few, ± spreading (except perichaetial bracts); cells of leaves on sterile plants or lower stem leaves broadly hexagonal, 10–11 μm or more wide. 30. *P. atropurpurea*
                8. Stomates ± deeply immersed.
                    10. Stems red, leaves small and erect, glossy green. 32. *P. vexans*
                    10. Stems green to orange; leaves larger, spreading, dull, often reddish. 33. *P. columbica*
    3. Annulus present; exothecial cells elongate-rectangular.
        11. Capsule erect; basal membrane low; segments narrow or rudimentary, not keeled.
            12. Endostome segments long, ± perforate; leaf margins recurved; cells rhombic, thick-walled. 15. *P. cardotii*
            12. Endostome segments variously reduced to absent; leaf margins plane; cells linear-rhomboidal; thin-walled. 16. *P. erecta*
        11. Capsule variously inclined; basal membrane low to high; segments broad and keeled or reduced.
            13. Exothecial cells long-rectangular, 60–90 μm long, with straight or slightly sinuose walls.
                14. Endostome segments narrowly or not at all split along the keel; cilia rudimentary or absent, rarely long.

15. Exostome teeth yellowish-white, coarsely papillose from apex to base. 10. *P. crudoides*
15. Exostome teeth brown to yellow-brown or hyaline, more coarsely papillose in the upper ½–⅔ than below.
16. Some or all plants with more than one seta per inflorescence. 8. *P. polycarpa*
16. Plants with one seta per inflorescence.
17. Plants with gemmae; exostome teeth ± blunt, papillose in the upper half, nearly smooth below. 13. *P. pseudo-barbula*
17. Plants without gemmae; exostome teeth acute or acuminate, coarsely papillose in the upper ⅓, gradually less papillose below.
18. Plants dull; leaf cells thick-walled.
19. Capsule 4–7 mm long; basal membrane ⅓–½ the exostome length; segments keeled. 3. *P. elongata*
19. Capsule 2–4 mm long; basal membrane to ⅓ the exostome length; segments scarcely keeled, often irregular. 3a. *P. elongata* var. *greenii*
18. Plants ± glossy; cells thin-walled.
20. Plants dioicous; leaves serrulate to serrate at the apex. 6. *P. bolanderi*
20. Plants paroicous; leaves coarsely serrate at the apex.
21. Plants very glossy (Canada and the U.S.). 7. *P. longicollis*
21. Plants slightly glossy, pale green (Mexico and Central America). 5. *P. oerstediana*

14. Endostome segments broadly split along the keel; cilia long.
22. Plants dioicous.
23. Plants growing with *Sphagnum*; leaves not decurrent; cells with thickened walls. 1. *P. sphagnicola*
23. Plants on alpine or subalpine soil; leaves longly decurrent; cells with thin to firm walls. 14. *P. ludwigii*
22. Plants paroicous.
24. Basal membrane low; segments narrow, scarcely keeled (though broadly perforate); cells lax and thin-walled, 12–20 μm wide. 9. *P. obtusifolia*
24. Basal membrane ½ the exostome length; segments broad and keeled; cells linear, 6–10 μm wide.
25. Leaves dull; cells with thickened walls. 2. *P. nutans*
25. Leaves slightly to strongly glossy; cells with thin walls.
26. Leaves broady lanceolate to elliptical, serrulate to serrate at the apex. 4. *P. cruda*
26. Leaves long-lanceolate, coarsely serrate at the apex. 5. *P. oerstediana*

13. Exothecial cells short rectangular, 25–60 μm long; with strongly sinuose walls.
27. Plants with axillary gemmae. Species 18–26
27. Plants without axillary gemmae (rhizoidal tubers sometimes present)
28. Plants robust; leaves longly decurrent; costa of perichaetial bracts much broadened at the base. 14. *P. ludwigii*
28. Plants slender; leaves little or not at all decurrent; costa of perichaetial bracts not much broadened at the base.
29. Plants very glossy; leaves coarsely serrate at the apex; cells 110–180 μm long. 27. *P. pacifica*
29. Plants not or slightly glossy; leaves serrulate to serrate at the apex; cells 65–120 μm long. 28. *P. lescuriana*

1. **Pohlia sphagnicola** (B. & S.) Lindb. & Arn., K. Svensk. Vet. Ak. Handl. 23: 53. 1890.

Bryum sphagnicola B. & S. *in* B. S. G., Bryol Eur. 4: 158. 1846. (Lectotype: BM–Schimp.).

Webera sphagnicola (B. & S.) Schimp., Coroll. 6. 1856.

Slender, dull-green plants generally scattered among *Sphagnum*. Stems 10–30 mm, simple or forking when sterile, simple or rarely innovating below the

inflorescence when fertile; leaves erect-spreading, distant, lanceolate, 1.0–1.6 mm long, entire to serrulae at the apices; upper cells hexagonal to rhomboidal, 25–60 μm long, 6–9 μm wide, thick-walled. Dioicous; perichaetial bracts to 3.5 mm long; perigonial bracts ± long-acuminate, erect to erect-spreading. Capsules inclined 90–145° from vertical, cylindric-pyriform, 3–5 mm long; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute to apiculate; exostome teeth orange-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 10–15 μm, almost smooth. Fig. 1.

Restricted to *Sphagnum* hummocks in bogs and fens; near sea level or montane. Northern Asia, Europe and North America; Oregon, Washington, Alberta, Manitoba, Quebec, Nova Scotia, Prince Edward Island, Newfoundland; Greenland. Map. 1.

Pohlia sphagnicola is circumboreal, but apparently rare throughout its range. It is restricted to *Sphagnum* hummocks but even there it is far less common than *P. nutans*. Habitat alone is not diagnostic for *P. sphagnicola*; in fact, Hedwig's type of *P. nutans* is mixed with a bit of *Sphagnum*. Bruch, Schimper and Gümbel described a variety *sphagnetorum* for *P. nutans* to cover forms growing with *Sphagnum* since they often have long stems and distant leaves.

Pohlia sphagnicola differs from *P. nutans* in having entire or weakly serrulate leaves, shorter cells, and smaller, more nearly smooth spores, in addition to dioicous inflorescences. The two are no doubt closely related, but the differences are, for the most part, consistent (Fig. 2). In an unpublished study at the University of Alberta, R. Belland made the same conclusions using different quantitative methods.

2. **Pohlia nutans** (Hedw.) Lindb., Musci Scand. 18. 1879.

Webera nutans Hedw., Spec. Musc. 168. 1801. (Lectotype: G: Hedw.–Schwaegr.).

Bryum trichodes Hedw., Spec. Mus. 168. 1801 (*nom. nud. in synon.—W. nutans* Hedw.).

B. interruptum Dicks., Pl. Crypt. Brit. fasc. 4. 13. 11f. 6. 1801. (Lectotype: BM–Dicks.).

B. nigricans Dicks., Pl. Crypt. Brit. fasc. 4. 15. 11f. 10. 1801. (Lectotype: BM–Dicks.).

B. sericeum Huds. *ex* With., Syst. Arr. Brit. Pl. ed. 4, 3: 822. 1801 (*nom. illeg. incl. spec. prior—W. nutans*).

Hypnum nutans (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3. 1803.

Bryum nutans (Hedw.) Turn., Musc. Hib. 117. 1804.

Webera bicolor Hoppe & Hornsch. *ex* Hornsch. 2: 102. 1819. (?Isotype: G: Hedw.–Schwaegr.).

Bryum insulare Houtt. *ex* Steud.,[1] Nomencl. Bot. 2: 88. 1924 (*nom. nud. in synon.—W. nutans* Hedw.).

Bryum subdenticulatum Brid., Bryol. Univ. 1: 634. 1826. (Lectotype: B–Brid.; Isotype: G: Hedw.–Schwaegr.).

Webera strangulata Nees *ex* Hueb., Musc. Germ. 428. 1833. (?Isotype: BM–Hampe).

Lamprophyllum nutans (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 25. 1871.

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[1] Article 46c of the international code of botanical nomenclature states that *ex* is appropriate in author citations only where the name was validly published. However, *ex* is used in this and similar citations for bibliographic completeness.

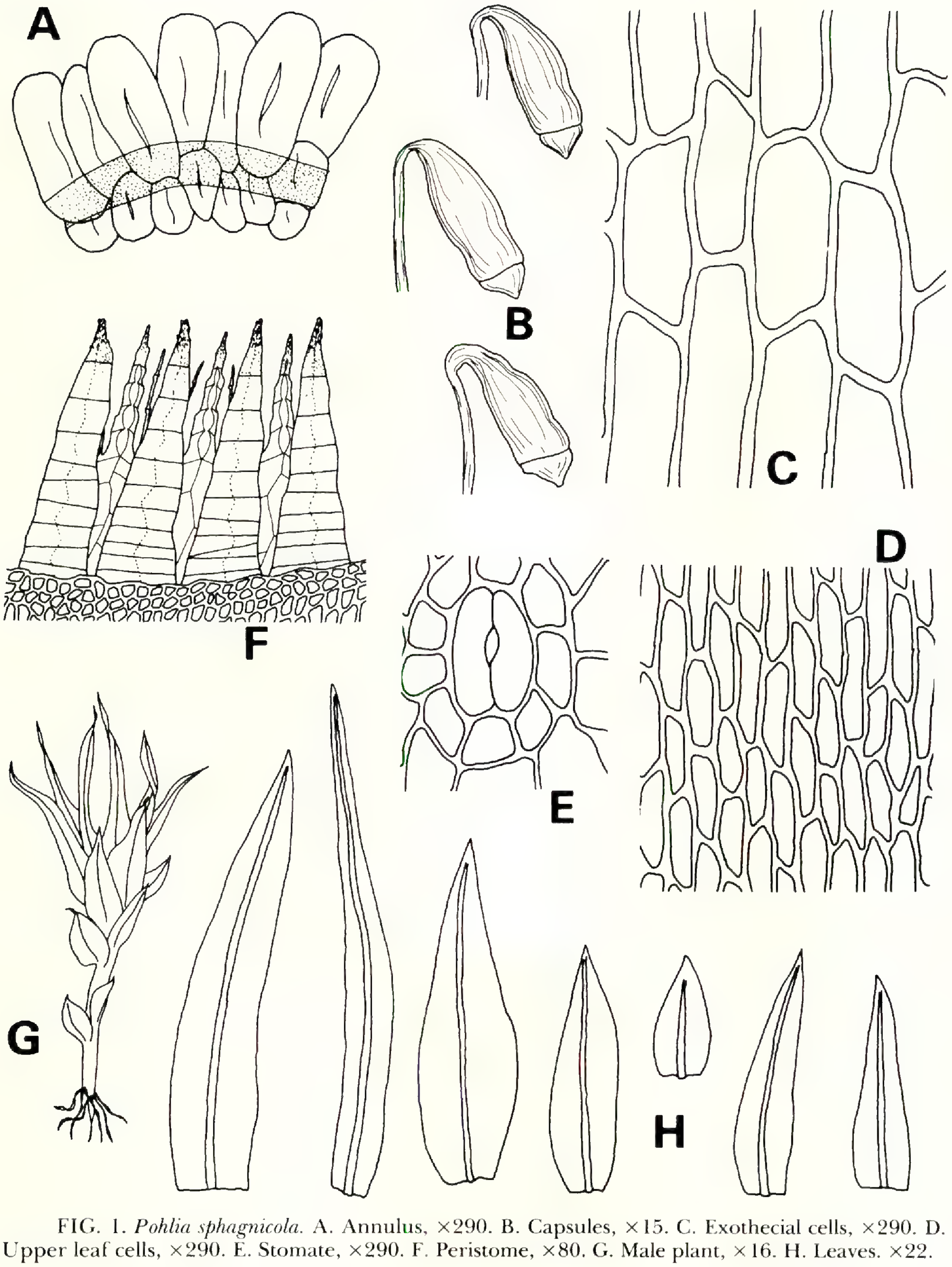


FIG. 1. *Pohlia sphagnicola.* A. Annulus, ×290. B. Capsules, ×15. C. Exothecial cells, ×290. D. Upper leaf cells, ×290. E. Stomate, ×290. F. Peristome, ×80. G. Male plant, ×16. H. Leaves. ×22.

Webera canaliculata C. Müll. & Kindb. *in* Macoun, Cat. Canad. Pl. 6: 113. 1892. (Lectotype: S–Kindb.; Isotype: BH).

Bryum cucullatiforme Kindb., Eur. N. Am. Bryin. 2: 387. 1897. (Lectotype: S–Kindb.: Isotype: BH).

Bryum nutans ssp. *macounii* Kindb., Eur. N. Am. Bryin. 2: 385. 1897. (Lectotype: S–Kindb.; Isotype: BH).

B. nutans ssp. *canaliculatum* (C. Müll. & Kindb. *in* Macoun) Kindb., Eur. N. Am. Bryin 2: 385. 1897.

Bryum canaliculatum (C. Müll. & Kindb. *in* Macoun) C. Müll., Gen. Musc. Fr. 221. 1901.

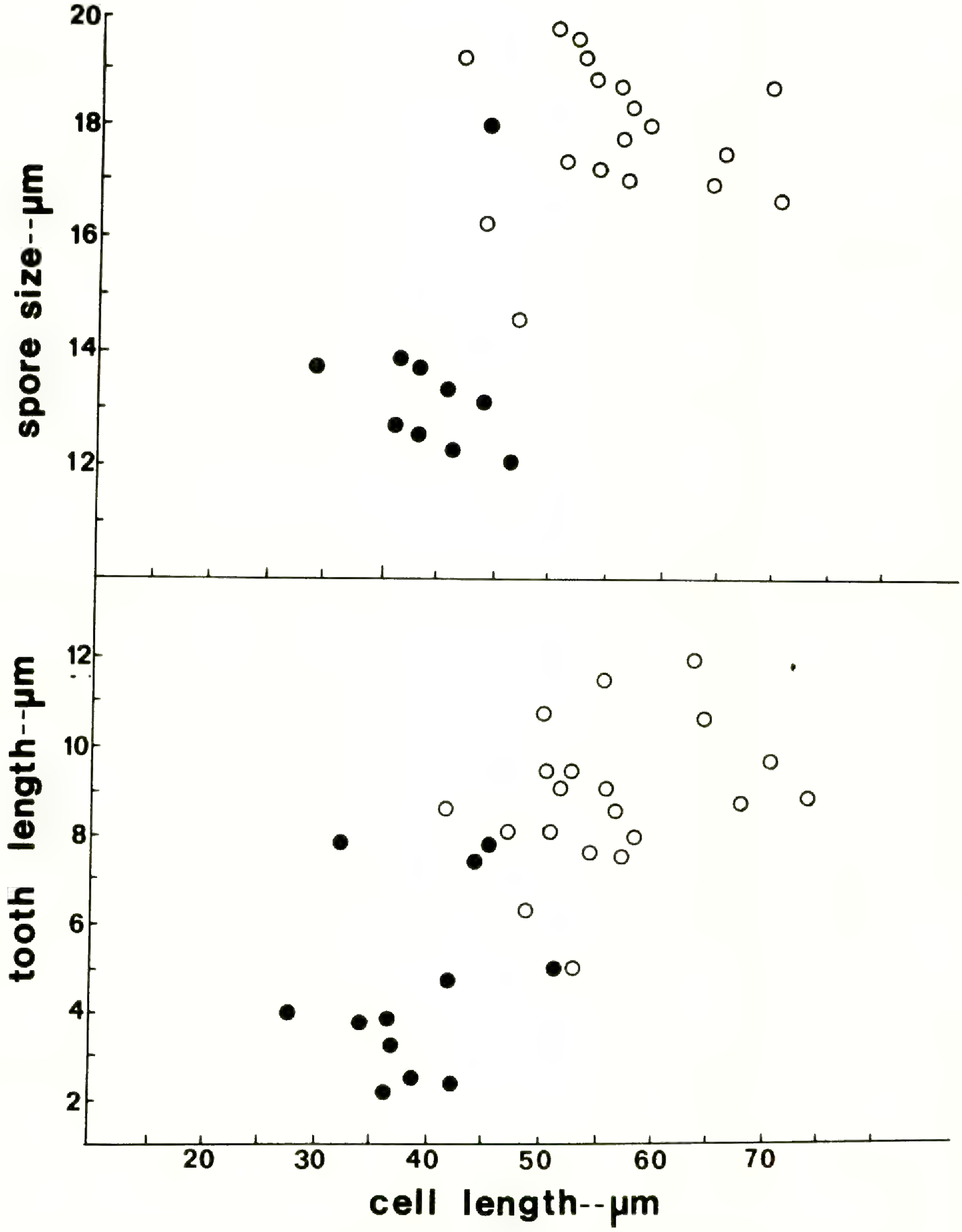


FIG. 2. Scatter diagrams comparing *Pohlia nutans* and *P. sphagnicola* with respect to leaf cell length, length of teeth on leaf margins, and spore diameter.

Bryum pertenellum Bryhn. & Ryan *in* Bryhn, Rep. Sec. Norw. Arctic Exp. Fram no. 11. 1906. (Lectotype: O).

Pohlia polygama Kindb., Rev. Bryol. 34: 92. 1907. (Lectotype: S–Kindb.).

Bryum graniticum Warnst. & Geh. *ex* Podp., Mag. Bot. Lapok. 18: 21. 1919. (*nom. inval. in synon.—P. nutans*).

Pohlia subdenticulata (Brid.) Podp. *in* Gyoerffy, Mag. Bot. Lapok. 18: 21. 1919.

Webera polygama (Kindb.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 360. 1924.

Bryum implexum Sw. *ex* Podp., Act. Ac. Sc. Nat. Morav. 17: 91. 1945 (*nom. nud. in synon.—P. nutans*).

Bryum compactum Aust., Bot. Gaz. 2: 111. 1877. (Lectotype: NY).

Slender to medium-size, dull-green plants scattered singly or forming extensive turfs. Stems 4–30 mm, simple or forking when sterile, simple or rarely innovating below the inflorescence when fertile. Leaves erect to spreading, crowded to distant, lanceolate, 0.8–1.6 mm long, serrate to serrulate near the apices; upper cells linear-rhomboidal, 50–90 μm long, thick-walled. Paroicous; perichaetial bracts to 4.0(–5.0) mm long. Capsules inclined 90–145° from vertical, cylindric-pyriform, 3–5 mm long; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute to apiculate; exostome teeth yellow to orange-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline, rarely yellow-brown; basal membrane ½ exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 16–22 μm, distinctly roughened. Fig. 3.

In rock crevices, on mineral soil, rotting logs, tree bases, roadbanks and mixed with *Sphagnum*; sea level to alpine. Across Canada and the northern United States, Europe and Asia; widespread at high latitudes of the Southern Hemisphere; south in North America to Maryland, Virginia, Missouri, Arizona, New Mexico and California (reported from Georgia and Arkansas); known in Mexico from only two localities (Potosí and Nevado de Toluca); apparently absent from the New World tropics. Map 2.

Exsiccati: Austin, Musci Appal. 510 as *B. elongatum* (UBC); Bauer, Musci Eur. Exs. 318–320 as *P. nutans* (ALTA), 909–910 as *P. nutans* (WTU), 911 as *P. nutans* f. *umbrosa* (WTU), 1095, 1096a & b as *P. nutans* v. *caespitosa* (WTU), 1097 as *P. nutans* v. *subglobosa* (WTU); Bauer, Bryoth. Bohem. 234 as *W. nutans* v. *sphagnetorum* (WTU); Boros, Plantae Hungar. Exs. 878 (CAS); Brotherus, Bryoth. Fenn. 335 as *P. nutans* v. *longiseta* (WTU); Drummond, Musci Amer. 262 as *B. nutans* (MICH); Grout, N. Am. Musci Perf. 23 as *P. nutans* (UC, CAS); Holzinger, Musci Acro. Bor.-Am. 143a & b as *W. commutata* (MICH, NY), 166 as *W. nutans* (MICH, UC, WTU), 167 as *W. nutans* v. *subdenticulata*, (MICH, UC, WTU), 524–525 as *W. nutans* (MICH, UC, WTU); Kobsch, Bryoth. Sax. 50 as *P. nutans* (MICH), 421 as *B. nutans* f. *elata* (MICH), 526 as *P. nutans* v. *caespitosa* (MICH); Macoun, Canad. Musci 160 as *W. nutans* (UC); Noguchi, Musci Jap. 840 as *P. nutans* (MICH); Rabenhorst, Bryoth. Eur. 329b as *B. nutans* (UC), 584 as *B. nutans* (UC); Sull. & Lesq., Musci Bor.-Am. (ed. 1) 179 as *B. nutans* (MICH), 178 as *B. nutans* (MICH), ed. 2, 267 as *B. nutans* (UC, MICH), 268 as *B. nutans* (MICH); Warnstorf, Märk. Laubm. 64 as *W. nutans* (CAS), 175 as *W. nutans* v. *sphagnitorum* (CAS).

Pohlia nutans is characterized by its thick-walled cells giving the plants a dull appearance, and paroicous inflorescence. The endostome is well-developed with keeled, broadly perforate segments and nodulose cilia. When sterile, plants are difficult to distinguish from *P. elongata,* except by habitat and range. Even some fruiting specimens approach *P. elongata* in having more narrowly perforate endostome segments, and (or) short cilia, making a definite determination impossible.

One poorly developed specimen from central Mexico (Nevado de Toluca, *Rzedowski 21676,* US) is unusual in having a yellow-brown endostome with rather narrowly split segments. The type of *Webera luisieri* Dix. from Madeira also appears to be decrepit *P. nutans* with a yellow endostome. I do not consider such forms worthy of nomenclatural recognition, at least on the basis of the rather poor material available.

Although rare, a few collections otherwise referable to *P. nutans* appear to be dioicous. Crum and Anderson (1981) reported one such New York collection (*Smith & Glider 43837*, as questionable *P. sphagnicola. Pohlia schimperi* (C. Müll.) Andr. is said to differ from *P. nutans* in its lush habit, red color, and dioicous inflorescence. North American specimens determined by Andrews as *P. schimperi* are all rather unexceptional *P. nutans,* and I have seen only one Alaskan collection (Peters Lake, *Steere 650725–21*) that agrees with the type of *P. schimperi.* The differences between the two species are not convincing. I have excluded *P. schimperi* from the North American flora, but have not placed it in the synonomy of *P. nutans* pending study of more collections. The many infra-

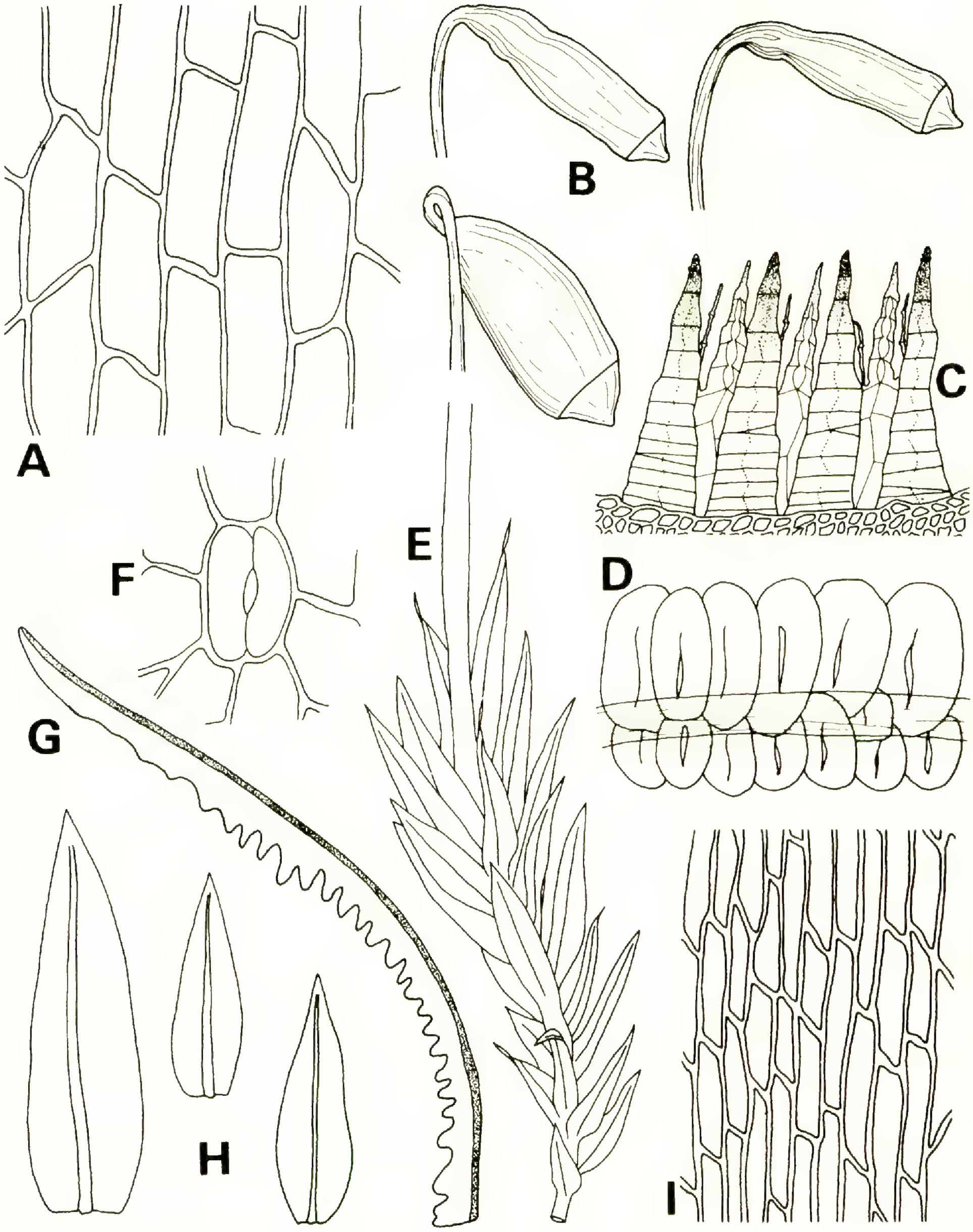


FIG. 3. *Pohlia nutans*. A. Exothecial cells, ×290. B. Capsules, ×15. C. Peristome, ×80. D. Annulus, ×290. E. Female plant, ×5. F. Stomate, ×290. G. Exostome tooth, lateral view showing relative thickness of dorsal and ventral plates and trabecula, ×250. H. Leaves, ×22. I. Upper leaf cells, ×290.

specific taxa proposed under *P. nutans* should be evaluated in the light of a world-wide study.

3. **Pohlia elongata** Hedw., Spec. Musc. 171. 1801.

Bryum cylindricum Dicks., Pl. Crypt. Brit. Fasc. 4, 12. 11f. 4. 1801. (Lectotype: BM–Dicks.).

Bryum elongatum (Hedw.) With., Syst. Arr. Brit. Pl. ed. 4, 3: 815. 1801.

Leskea elongata (Hedw.) Web. & Mohr, Ind. Musc. Pl. Crypt. 3. 1803.

Mnium elongatum (Hedw.) P. Beauv., Prodr. 75. 1805.

M. pohlia Hoff. *ex* P. Beauv., Prodr. 75. 1805. (*nom. nud. in synon.—M. elongatum*).

Pohlia arcuata Hoppe & Hornsch. *ex* Hornsch., Flora 2: 98. 1819. (Lectotype: GZU-Hoppe).

P. brachycarpa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 96. 1819. (Lectotype: GZU-Hoppe).

P. tenella Hoppe & Hornsch. *ex* Hornsch., Flora 2: 95. 1819. (Lectotype: GZU-Hoppe).

Webera caespitosa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 102. 1819. (Lectotype: GZU-Hoppe).

Pohlia acuminata Hoppe & Hornsch. *ex* Hornsch., Flora 2: 94. 1819. (Lectotype: GZU: Hoppe; Isotype: G: Hedw.–Schwaegr.).

P. polymorpha Hoppe & Hornsch. *ex* Hornsch., Flora 1: 100. 1819. (Lectotype: GZU: Hoppe).

P. affinis Hoppe & Hornsch. *ex* Hornsch., Flora 2: 97. 1819. (Lectotype: GZU: Hoppe).

P. pulchella Hoppe & Hornsch. *ex* Hornsch., Flora 2: 95. 1819. (Lectotype: GZU: Hoppe; Isotype: G: Hedw.–Schwaegr.).

P. xanthocarpa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 97. 1819. (Lectotype: GZU: Hoppe).

Webera macrocarpa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 104. 1819. (Isotype: G: Hedw.–Schwaegr.).

Pohlia cylindrica (Dicks.) Hornsch., Flora 2: 93. 1819.

P. recognita Reichenb., Flora 5: 540. 1822 (*nom. nud. in synon.—P. elongata*).

P. minor var. *affinis* (Hoppe & Hornsch. *ex* Hornsch.) Brid., Bryol. Univ. 7: 612. 1826.

P. elongata var. *cylindrica* (Dicks.) Brid., Bryol. Univ. 7: 610. 1826.

Webera alpina var. *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Brid., Bryol. Univ. 7: 627. 1826.

Webera elongata var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Schwaegr., Suppl. Spec. Pl. ed. 4, 5: 49. 1830.

P. elongata var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 473. 1833.

P. polymorpha var. *affinis* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 470. 1833.

P. polymorpha var *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 470. 1833.

P. brachycarpa var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Schwaegr. *ex* Hueb., Musc. Germ. 717. 1833.

Bryum boissieri D. Not., Syll. 134. 1838. (Lectotype: R: De Not.).

B. polymorphum (Hoppe & Hornsch. *ex* Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 296. 1838.

B. elongatum var. *macrocarpum* (Hoppe & Hornsch. *ex* Hornsch.) B. & S. *in* B. S. G., Bryol. Eur. 4: 102. 1839.

B. acuminatum (Hoppe & Hornsch. *ex* Hornsch.) B. & S., Bryol. Eur. 4: 91. 1839.

Bryum alpinum var. *macrocarpum* (Hoppe & Hornsch. *ex* Hornsch.) Lesq., Mem. Soc. Sc. Neuchâtel. 3: 37. 1845.

?*B. integridens* C. Müll., Syn. 1: 338. 1848 (type not seen).

B. spectabile C. Müll., Syn. 2: 583. 1851. (Lectotype: H–Br.).

Webera acuminata (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

W. acuminata var *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

W. acuminata var. *tenella* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

W. elongata var. *macrocarpa* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

Webera polymorpha (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

W. polymorpha var. *affinis* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

W. polymorpha var. *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

Lamprophyllum elongatum (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 27. 1871.

W. spectabilis (C. Müll.) Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872.

?*W. integridens* (C. Müll.) Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872.

W. cylindrica Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872. (Isotype: NY; ?Isotype: BM).

Bryum cylindricum Mont. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872 (*nom. inval. in synon.–W. cylindrica*).

Webera muelleriana Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872. (?Isotype: BM: Schimp.).

W. gracilicarpa Hampe, Vid. Medd. Naturh. For. Kjoebenh. ser. 3, 6: 149. 1875.

W. ambigua Limpr., Laubm. Deutschl. 2: 237. 1891. (Lectotype: BP–Limpr.).

B. elongatum ssp. *ambiguum* (Limpr.) Kindb., Eur. N. Am. Bryin. 2: 390. 1890.

B. elongatum ssp. *acuminatum* (Hoppe & Hornsch. *ex* Hornsch.) Kindb., Eur. N. Am. Bryin. 2: 390. 1890.

Bryum muellerianum (Schimp. *ex* Besch.) C. Müll., Gen. Musc. Fr. 220. 1901.

Bryum ambiguum (Limpr.) Kindb. *ex* Par., Ind. Bryol. Suppl. 56. 1900 (*nom. inval. in synon.–B. elongatum* spp. *ambiguum*).

Pohlia ambigua (Limpr.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

P. muelleriana (Schimp. *ex* Besch.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

P. spectabilis (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

?*P. integridens* (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

P. elongata var. *macrocarpa* (Hoppe & Hornsch. *ex* Hornsch.) Herz., Bot. Jahrb. 47: 482. 1912.

P. acuminata var. *tenella* (Hoppe & Hornsch. *ex* Hornsch.) Amann, Fl. Mouss. Suisse 2: 178. 1919.

P. acuminata var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Amann, Fl. Mouss. Suisse 2: 178. 1919.

P. polymorpha var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) C. Jens., Danm. Moss. 2: 392. 1923.

Pohlia zacatecana Williams, Bryol. 26: 33. 4. 1923. (Isotype: US).

Webera zacatecana (Williams) Thér., Smiths. Misc. Coll. 81: 7. 1928.

Webera polymorpha var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) C. Jens., Skand. Bladmfl. 166. 1939.

Pohlia polymorpha ssp. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Podp., Consp. 331. 1954.

P. polymorpha var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Podp., Consp. 331. 1954.

P. minor var. *tenella* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor var. *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor ssp. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor var. *pulchella* (Hoppe & Hornsch. *ex* Hornsch.) Dem. & Wilz., Bull. Jard. Bot. Nat. Belg. 48: 449. 1978.

Slender to medium size, dull-green plants forming small populations, often in rock crevices. Stems 5–25 mm, simple or forking when sterile, frequently innovating below the inflorescence when fertile. Leaves erect to erect-spreading, crowded to distant, lanceolate, 0.9–1.7 mm long, serrulate to serrate near the apices; upper cells rhomboidal to linear-hexagonal, 45–85 μm long, thick-walled. Paroicous or rarely autoicous; perichaetial bracts little to strongly differentiated, to 3.5 mm; perigonia in autoicous plants terminal on short to elongate side branches, the perigonial bracts shortly acute. Capsules inclined 10°–90° from vertical, shortly to longly cylindric-pyriform, 3.5–7.0 mm long; exothecial cells elongate-rectangular, 50–110 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute; exostome teeth yellow to brown, acute-triangular, most coarsely papillose near the apex, bordered, trabeculate; endostome hyaline; basal membrane ⅓–½ the exostome length; segments keeled but narrowly perforate; cilia short, absent, rarely long and ± nodulose. Spores 16–23 μm; distinctly roughened. Fig. 4, 5.

Roadbanks and streambanks; frequent in rock crevices in arctic or alpine regions; reportedly epiphytic in New Guinea. Widespread at high latitudes across the three northern continents. In North America, apparently absent from the Cascade-Sierra Nevada system of the western United States, but extending southward in the Appalachians to Tennessee and North Carolina. Ranging in the Rockies from Alaska to Arizona, and extending in the mountains through Mexico, Central America and, through scattered records, to southern South America; Africa, China, Nepal, S. E. Asia, Phillipines, Japan, and New Guinea. Map 3.

Exsiccati: Austin, Musci Appal. (Suppl. 1) 510 as *B. elongatum* (CANM, NY); Bauer, Musci Eur. Exs. 903 as *P. acuminata* (WTU); Bauer, Bryoth. Bohem. 233 as *W. elongata* v. *oder* f. *pseudolongicolla* (BM); Erbar, Crittogam. Ital. 609 as *W. elongata* (UC, NY); Fleischer, Musci Frond. Arch. Indici 285 as *W. brachydontea* (NY); Grout, N. Am. Musci Perf. 398 as *P. elongata* (CANM, MICH, UC); Hartman, Bryac. Scand. 376 as *W. elongata* (BH); Holzinger, Musci Acro. Bor.–Am. 145 as *W. elongata* (CANM, MICH, NY, UC); Husnot, Musci Gall. 461 as *W. elongata* (BH, BM, NY); Macoun, Canad. Musci 521 as *W. acuminata* (MICH), 806 as *W. acuminata* (CANM); Noguchi & Hattori, Musci Jap. 386 as *P. elongata* (ALTA, BH, MICH, NY); Pringle, Plant. Mex. 10623 & 10648 as *W. cylindrica* (MICH, MO); Rabenhorst, Bryoth. Eur. 275 as *W. elongata* (NY, UC), 360 as *W. elongata* (NY, UC); Schultz, Flora Gall. et Germ. Exs. 1185 as *B. elongatum* (BM); Sull. & Lesq., Musci Bor. Amer. (ed. 1) 177 as *B. elongatum* (BH, MICH, NY), (ed. 3) 266 as *B. elongatum* (BH, MICH, NY, UC), 270 as *B. ludwigii* (BH).

Pohlia elongata is distinguished from related species by its (usually) paroicous inflorescence, longly cylindric capsules (4–7 mm), and especially the narrowly or scarcely perforate endostome segments. Unlike *P. longicollis* and *P. bolanderi*, which have similar peristomes, the leaves are dull with cell walls incrassate. The sexuality of *P. elongata* var. *elongata* is almost uniformly paroicous, although a few specimens, including the type of *Webera ambigua* Limpr., are autoicous.

Capsule size and shape are extremely variable. Mexican and Central American plants generally known as *P. spectabilis* are characterized by exceptionally long, narrow capsules. However, other than in exothecial cell length which is obviously correlated in development with capsule length, such plants can scarcely be distinguished consistently from more typical *P. elongata*. Although a somewhat coherent distribution in Mexico and Central and northern South America suggests at least limited genetic distinctiveness for *P. spectabilis*, frequent intergradation makes recognition of two taxa impractical. A specimen from Virginia

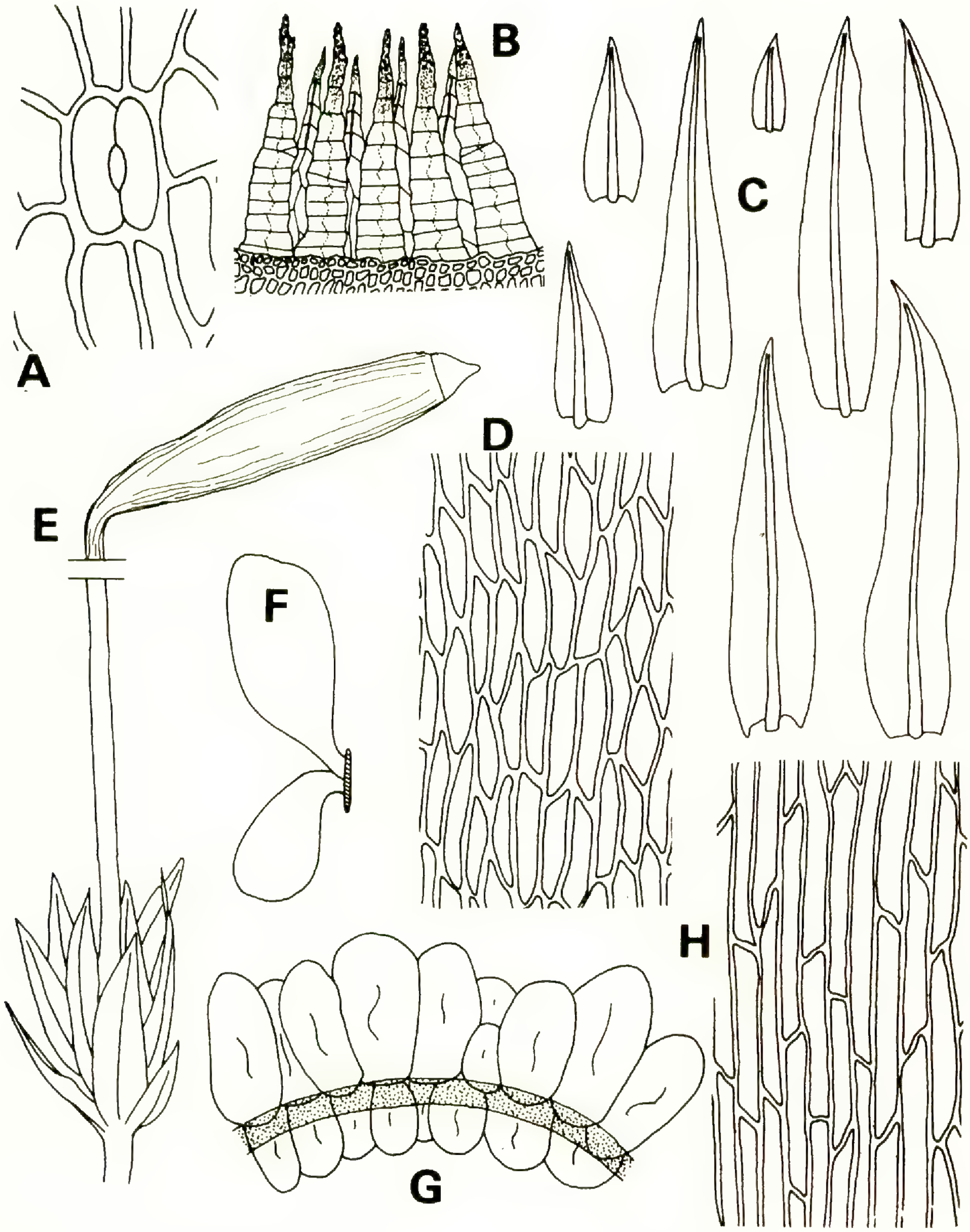


FIG. 4. *Pohlia elongata*. A. Stomate, ×290. B. Peristome, ×80. C. leaves, ×22. D. Upper cells of branch leaf, ×290. E. Habit, ×7. F. Lateral view of annular cells, ×290. G. Annulus, ×290. H. Upper cells of perichaetial bract, ×290.

(*Brown*, 1890, UBC) also approaches *P. spectabilis*. In Mexico, as both the "spectabilis" and typical expressions, *P. elongata* is more common then anywhere else in North America.

At the other extreme, scattered collections of *P. elongata* from arctic, alpine, or other harsh habitats are characterized by a suite of distinctive attributes. These plants can be distinguished as the var. *greenii*.

3b. **Pohlia elongata** var. **greenii** (Brid.) Shaw, comb. nov.

Pohlia minor Schwaegr., Spec. Musc. Suppl. 1: 70. 64. 1816. (Lectotype: G: Hedw.–Schwaegr.; Isotype: B–Brid.).

P. gracilis Hoppe & Hornsch. *ex* Hornsch., Flora 2: 100. 1819. (Lectotype: G: Hedw.–Schwaegr.).

P. polyseta Hoppe & Hornsch. *ex* Hornsch., Flora 2: 99. 1819. (?Isotype: BM).

P. curviseta Hoppe & Hornsch. *ex* Hornsch., Flora 2: 98. 1819. (Lectotype: GZU: Hoppe; ?Isotype: G: Hedw.–Schwaegr.; ?Isotype: NY).

P. greenii Brid., Mant. Musc. 115. 1819. (Lectotype: B: Brid.).

P. minor Schwaegr. var. *greenii* (Brid.) Brid., Bryol. Univ. 1: 612. 1826.

P. elongata var. *minor* (Schwaegr.) Hartm., Handb. Skand. Fl. ed. 2L 336. 1832.

P. polymorpha var. *minor* (Schwaegr.) Hueb., Musc. Germ. 470. 1833.

P. polymorpha var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 470. 1833.

Bryum elongatum var. *minus* (Schwaegr.) Hartm., Handb. Skand. Fl. ed. 3: 296. 1838.

Webera gracilis (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

W. acuminata var. *minor* (Schwaegr.) Schimp., Coroll. 64. 1856.

W. acuminata var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

Bryum nudicaule Lesq., Mem. Calif. Ac. Sc. 1. 21. 1868.

Webera nudicaulis (Lesq.) Lesq. & James, Man. N. Am. Moss. 220. 1884.

Pohlia polymorpha var. *gracilis* (Hoppe & Hornsch. *ex* Hornsch.) Braithw., Brit. Moss Fl. 2: 145. 1892.

Pohlia nudicaulis (Lesq.) Broth. *ex* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

P. brachycarpa var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Schwaegr. *ex* Par., Ind. Bryol. ed. 2, 5: 105. 1906.

P. acuminata var. *minor* (Schwaegr.) Amann, Fl. Mouss. Suisse 3: 178. 1919.

P. acuminata var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Amann, Fl. Mouss. Suisse 3: 178. 1919.

P. minor var. *gracilis* (Hoppe & Hornsch. *ex* Hornsch.) Wijk et Marg., Taxon 8: 74. 1959.

Tiny, dull-green plants scattered singly or in small populations. Stems very short, with 5–10 leaves. Leaves scarcely 1 mm long, broadly lanceolate; upper cells rhombic, 35–65 μm long, thick-walled. Paroicous, autoicous or rarely dioicous; perichaetial bracts undifferentiated, broadly lanceolate, to 1.5 mm long; perigonia in dioicous plants terminal on short, simple stems, the bracts shortly and broadly acute, erect. Capsules inclined 145°–190° from vertical segments broadly pyriform, 2–3.5 mm long; basal membrane low, up to ⅓ the exostome length, segments often irregular, linear, scarcely keeled, narrowly perforate to entire; cilia absent. Fig. 5.

Rock crevices in tundra areas, less frequently on exposed soil. Alaska, Washington, California, Colorado, Utah, Newfoundland; Greenland. Reported from northern Europe. Map 4.

Although no single character is diagnostic, several morphological attributes distinguish the var. *greenii* from so-called typical expressions: smaller overall size; shorter, broader leaves, more strongly inclined, broader, shorter capsules, low basal membrane, irregular segments, and complete lack of cilia.

Ironically, it is Hoppe and Hornschuch's extensive list of "new species" that provides the most persuasive argument against recognizing the var. *greenii* at the specific level. With over ten taxa, they (Hoppe and Hornschuch *ex* Hornschuch 1819) typified practically every conceivable intermediate between the long and short capsule forms. However, sporophytic and gametophytic differences between the varieties, coupled with geographic differences, warrant separation, at least on the basis of North American plants. Unlike *P. spectabilis*, the var. *greenii*

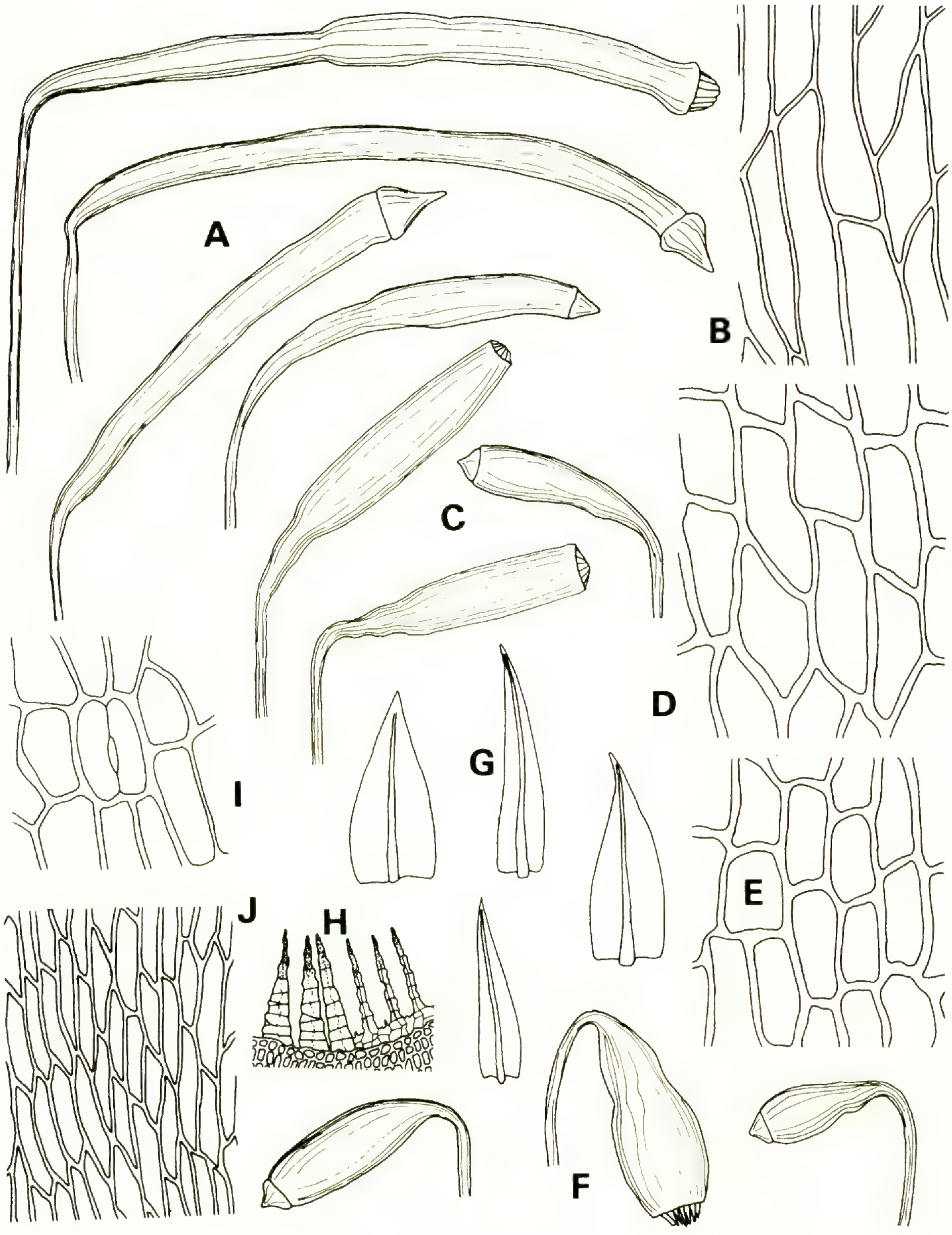


FIG. 5. A–D. *Pohlia elongata* var. *elongata*. A. Capsules, Mexican plants commonly called *P. spectabilis*, ×13. B. Exothecial cells from capsules as in A, ×230. C. Capsules, typical North American plants, ×13. D. Exothecial cells from capsules as in C, ×230. E–J. *Pohlia elongata* var. *greenii*. E. Exothecial cells from capsules as in F, ×230. F. Capsules, ×13. G. Leaves, ×18. H. Peristome, ×58. I. Stomate, ×230. J. Upper leaf cells, ×230.

differs from the var. *elongata* in more than just capsule shape, and notably so in endostome morphology. *Webera carneoides* Dix & Badw. of the Himalayas represents the var. *greenii* at its extreme. The plants are minute, with capsules scarcely longer than wide.

It is difficult to typify the var. *greenii* because so many names are available representing the extensive intergradation that occurs between plants with long and short capsules. Most of the old types are fragmentary and could scarcely endure yet one more peristome dissection. My concept of the var. *greenii* is the

short capsule-reduced endostome form at or near its extreme (Fig. 5). Extensive variation in capsule shape is allowed in the var. *elongata*. The names *P. polymorpha* and *P. acuminata* have been used for plants with relatively short capsules. Specimens in Hoppe's herbarium with these names have intermediate to elongate capsules (e.g. Fig. 5c), falling within the range of the var. *elongata*.

4. **Pohlia cruda** (Hedw.) Lindb., Musci Scand. 18. 1879.

Mnium crudum Hedw., Spec. Musc. 189. 1801. (Lectotype: G: Hedw.–Schwaegr.).
Hypnum crudum (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3: 1803.
Webera cruda (Hedw.) Fuernr., Flora 12(Ergbl. 2): 35. 1829.
Lamprophyllum crudum (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 87. 1871.
Webera cruda var. *nivalis* Podp. *ex* Herz., Wien. Bot. Zeitschr. 93: 45. 1944. (Lectotype: BRNM).

Robust to slender, shiny, pale whitish-green plants generally forming small populations. Stems 5–20 mm, simple or forking when sterile, usually simple when fertile. Leaves wide-spreading to erect-spreading, distant to crowded, lanceolate to elliptic, sometimes ± asymmetric, 1.0–2.0 mm long, serrate to serrulate at the apices; upper cells linear-rhomboidal, 70–120 μm long, 6–9 μm wide, thin-walled. Paroicous or dioicous; perichaetial bracts variable, lanceolate to linear, to 4.0–5.0 mm long; perigonial bracts longly acuminate, to 5.0 mm long. Capsules inclined 10°–135° from vertical, narrowly or rarely broadly cylindric-pyriform, 4–6 mm long; exothecial cells elongate-rectangular, 40–80 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic; exostome yellow-brown to red-brown; acute-triangular, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 18–26 μm, rather coarsely papillose. Fig. 6.

Soil of roadbanks, streambanks, tundra, often in crevices under rocks or exposed roots; rarely on rotting wood. Circumboreal; across northern North America south to California, Arizona, Tennessee and North Carolina; Mexico (Puebla, Tlaxcala, Mexico); Chile; Antarctica; New Zealand; Auckland Islands; Hawaii; India; Japan; reported from eastern Asia. Map 5.

Exsiccati: Allen, Mosses of the Cascade Mts. 58 as *B. crudum* (MICH); Bauer, Musci Eur. Exs. 311 as *P. cruda* (ALTA); Drummond, Musci Amer. 269 as *B. crudum* (MICH, UC); Grout, N. Am. Musci Perf. 398a as *P. elongata* (MICH), 443a as *P. cruda* (CAS, MICH, UC), 443b as *P. cruda* (MICH); Holmen, Bryoph. Dan. Exs. 155 as *W. cruda* (ALTA, UC); Holzinger, Musci Acro. Bor.–Am. 144 as *W. cruda* v. *minor* (MICH, UC); Kobsch, Bryoth. Sax. 336 as *W. cruda* (MICH); Macoun, Canad. Musci 161 as *W. cruda* (UC), 446 as *W. cruda* (MICH), 637 as *W. micro-apiculata* (MICH); Noguchi, Musci Jap. 1134 as *P. cruda* (MICH); Rabenhorst, Bryoth. Eur. 1024 as *W. cruda* (CAS); Sull. & Lesq., Musci Bor. Am. (ed. 1) 179b as *B. crudum* (MICH); Warnstorf, Märk. Laubm. 270 as *W. cruda* (CAS).

Readily distinguished by its pale, whitish-green color and strong gloss, *P. cruda* is not to be confused with any other *Pohlia*. It is further characterized by the longly cylindric capsules and well-developed endostome with broadly perforate segments and long cilia.

I have seen a few sterile *Pohlia* collections with elongate stems (to 2 cm) and glossy pale-green leaves. These are distinctive, with the leaves lanceolate, erect, and overlapping. One such gathering (N.Y., Westchester Co., *Shaw*, 26 Dec. 1981, MICH) grew on seepy granitic rock in beech-maple forest. The habitat, as well as the aspect of the plants, brought *Mielichhoferia* to mind. In the absence of sporophytes, these are interpreted as *P. cruda*, mostly by default. Ecologically and morphologically this expression is well characterized.

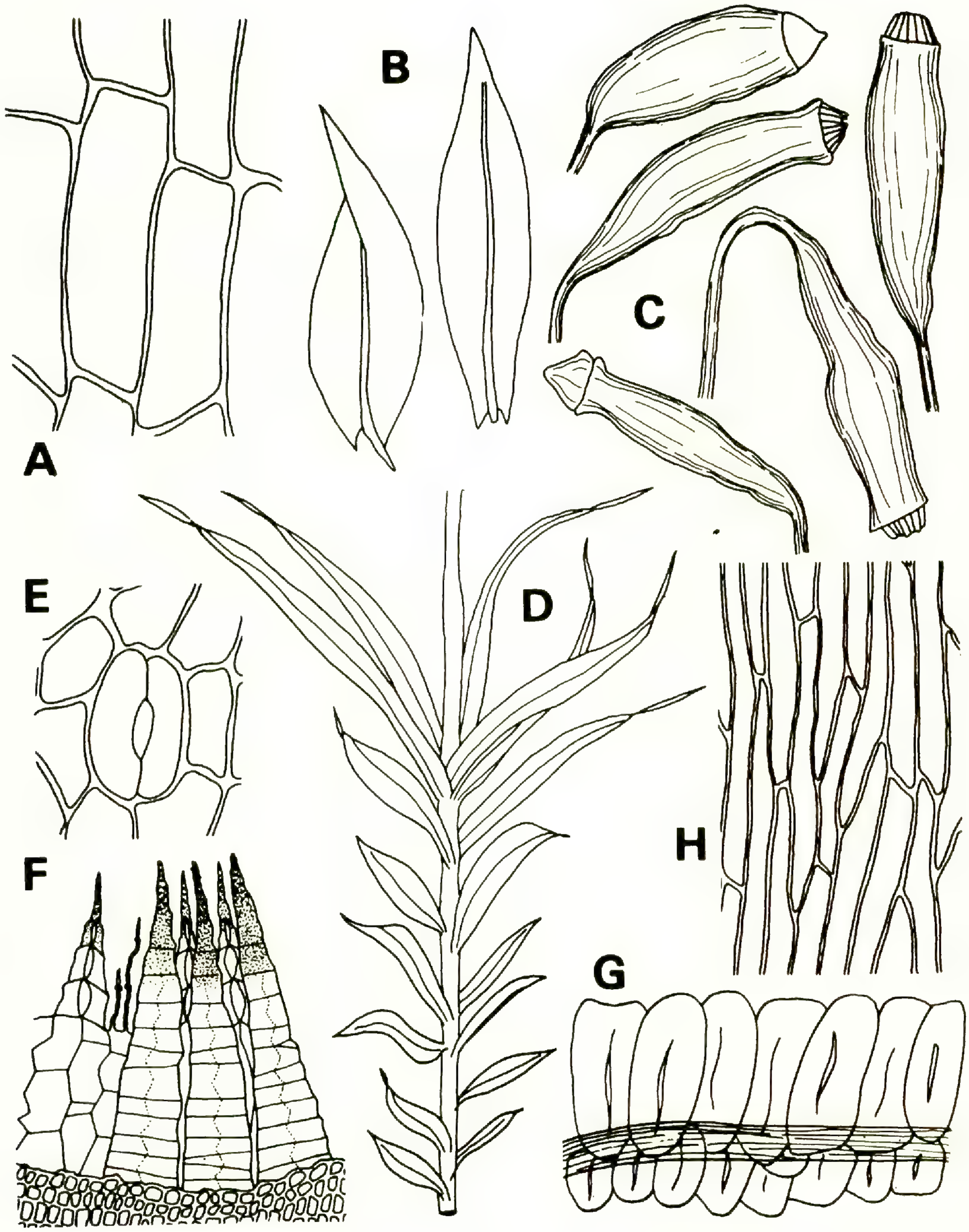


FIG. 6. *Pohlia cruda*. A. Exothecial cells, ×290. B. Leaves, ×22. C. Capsules, ×15. D. Habit, ×4.5. E. Stomate, ×290. F. Peristome, ×80. G. Annulus, ×290. H. Upper leaf cells, ×290.

5. **Pohlia oerstediana** (C. Müll.) Shaw, comb. nov.

Bryum oerstedianum C. Müll., Syn. 2: 583. 1851. (Lectotype: H–Br; Isotype: BM–Hampe).

Webera oerstediana (C. Müll.) Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 128. 1875.

Bryum seleri C. Müll., Bull. Herb. Boiss. 5: 181. 1897. (Lectotype: H–Br).

Pohlia seleri (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

Webera orizabensis Card., Rev. Bryol. 40: 38. 1913. (Holotype: PC).

Robust, shiny to dull, pale whitish-green plants often in deep turfs. Stems (5–)10–30 mm, simple or forking when sterile, generally simple when fertile.

Leaves erect to erect-spreading, crowded and imbricate, lanceolate, 1.5–2.5 mm long, coarsely serrate near the apices; upper cells linear-rhomboidal, 70–135 μm long, 6–11 μm wide, thin-walled. Paroicous; perichaetial bracts gradually enlarged, to 3.5 mm long. Capsules inclined 10°–100° from vertical, longly cylindric, to ca. 6 mm long; exothecial cells elongate-rectangular, 40–80 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows; opercula conic; exostome yellow to red-brown, acute-triangular, bordered, trabeculate; endostome hyaline; basal membrane ½ the height of exostome teeth; segments keeled, broadly to narrowly perforate; cilia long to short, sometimes nodulose. Spores 19–25 μm, rather coarsely papillose. Fig. 7.

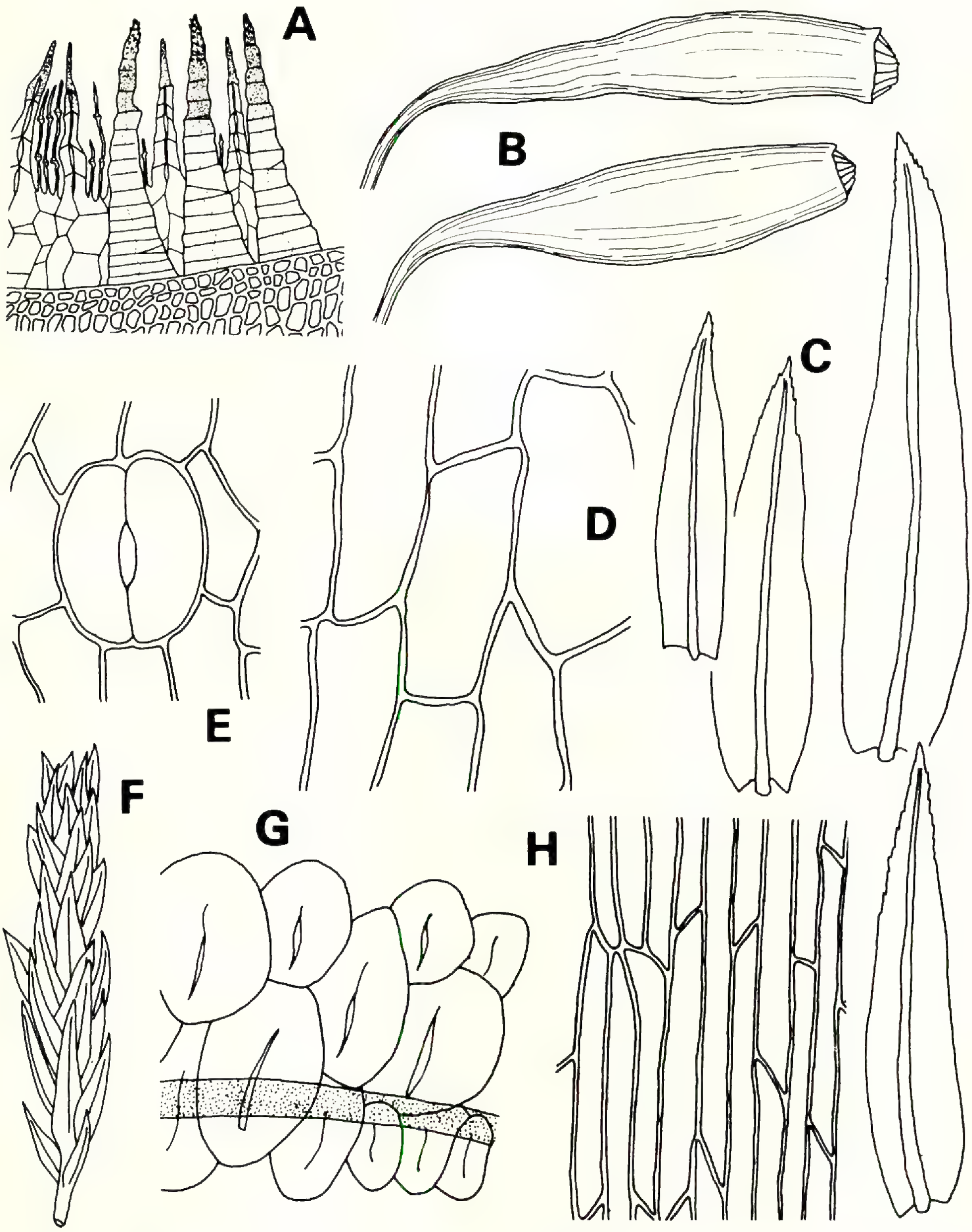


FIG. 7. *Pohlia oerstediana*. A. Peristome, ×80. B. Capsules, ×15. C. Leaves, ×22. D. Exothecial cells, ×290. E. Stomate, ×290. F. Habit, ×4. G. Annulus, ×290. H. Upper leaf cells, ×290.

Soil, moist rocks, tree bark, rotting logs, at high elevations in Oak-Pine forests. Mexico (Hidalgo, Mexico, Oaxaca, Puebla, Tlaxcala, Veracruz). Guatemala (San Marcos, Huehuetenango) and Costa Rica (Volcán Irazu). Map 6.

Exsiccati: Pringle, Plant. Mex. 10548 as *W. cylindrica* (FH).

Pohlia oerstediana is distinguished from *P. cruda* by its larger size, and less glossy leaves that are coarsely serrate near the apex. It is exceptionally robust in microscopic details as well as overall habit (Fig. 7). This species seems to be more common than *P. cruda* in Mexico and Central America, with *P. cruda* more or less restricted to alpine habitats. Most or all records of *P. cruda* given by Bartram (1949) should be referred to *P. oerstediana*.

I have seen few capsules of *P. oerstediana* with intact peristomes, but the segments seem to be variable with respect to perforation. The Asian *Webera laticuspis* Broth. is very similar to *P. oerstediana* gametophytically and has narrowly perforate segments. Such a disjunction, though interesting, is not unheard of among mosses (e.g. *Aoengstroemia orientalis* Mitt.).

6. **Pohlia bolanderi** (Sull.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.
Bryum bolanderi Sull., Mem. Calif. Acad. Sci. 1. 22: 1868.(Lectotype: NY).

Slender to medium-size, glossy green plants in compact turfs. Stems 3–10 (–20) mm, simple or forking when sterile, simple when fertile. Leaves erect to erect-spreading, crowded and imbricate, lanceolate, 1.0–1.6 mm long, serrate to serrulate at the apices; upper cells linear-rhomboidal, 55–100 μm long, 6–9 μm wide, thin-walled. Dioicous; perichaetial bracts scarcely differentiated, to 2 mm long; perigonial bracts shortly acute, erect. Capsules inclined 35°–90° from vertical, elongate-cylindric, 3–5 mm long; exothecial cells elongate-rectangular, 40–85 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute; exostome teeth yellow to yellow-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ⅓–½ the exostome length; segments keeled but narrowly perforate; cilia short, rarely long. Spores 16–26 μm, distinctly roughened. Fig. 8.

Rather dry alpine or subalpine soil, less commonly along streams, high montane to alpine. Apparently endemic to western North America; British Columbia; Washington, Oregon, California, Nevada. Map 7.

In addition to the dioicous inflorescence, *P. bolanderi* is distinguished from its close relative, *P. longicollis,* by the smaller overall size and less coarsely serrate leaves. The distinctive geographic range of *P. bolanderi* gives meaning to these relatively slight morphological differences. The distributions of the two species overlap only in southern British Columbia. Reports of *P. longicollis* from California, Oregon, and Washington are referable to *P. bolanderi*.

6a. **Pohlia bolanderi** var. **seriata**, Shaw, var. nov.

Plantae erectae, strictae, dense confertae, plerumque steriles. Folia pallida, dense seriata, imbricata, lanceolata, carinata. Flores dioici. Perichaetia parva, inconspicua, bracteis paucis.

Dull, whitish plants often in deep, luxuriant turfs. Stems erect, up to 5.0 cm high. Leaves ± distinctly arranged in 4–5 vertical rows, pale green to whitish, erect to erect-spreading. Dioicous; perichaetia terminal on simple stems, inconspicuous, the bracts not differentiated from lower leaves. Perigonia and sporophytes as in the var. *bolanderi*. Fig. 9.

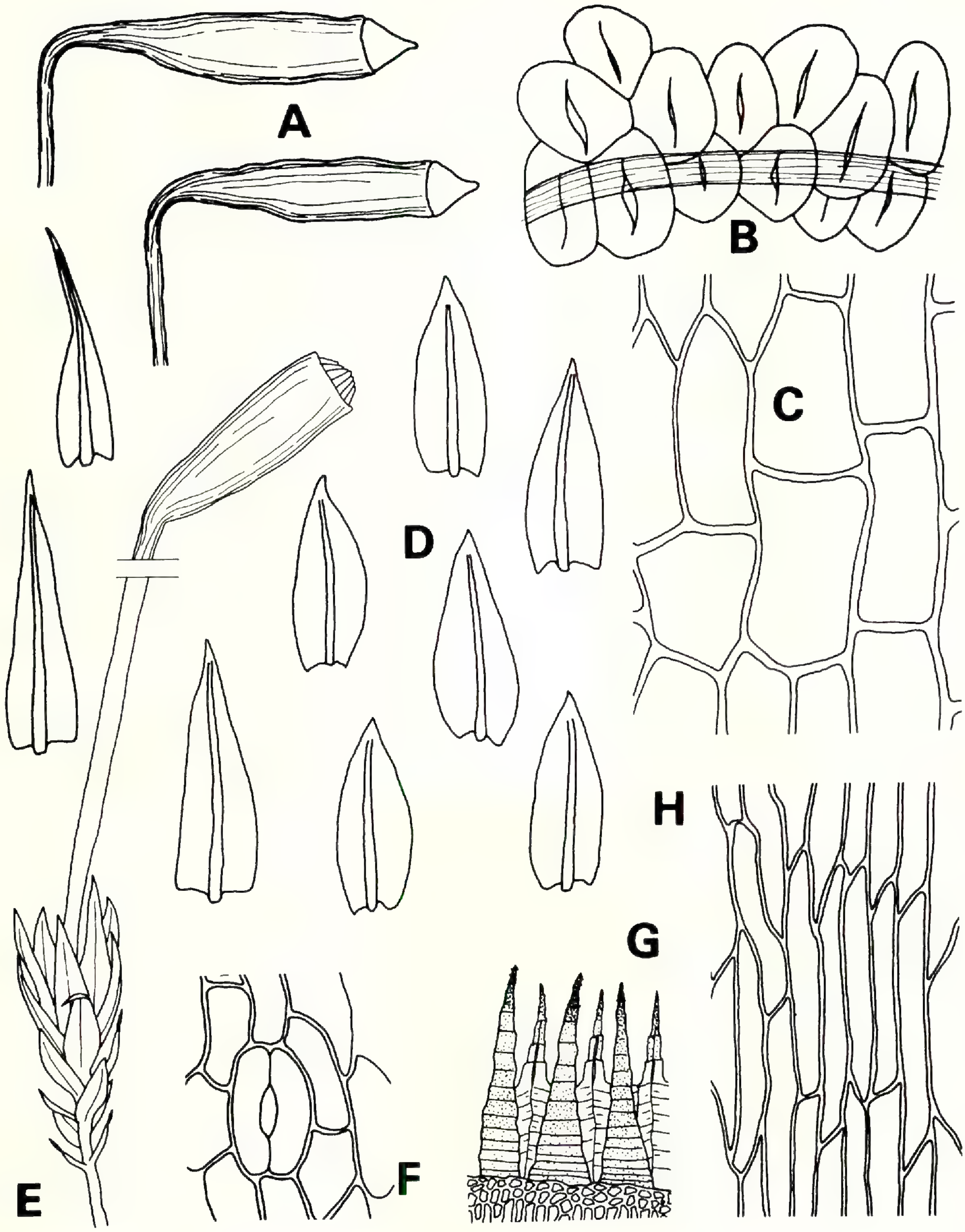


FIG. 8. *Pohlia bolanderi*. A. Capsules, ×15. B. Annulus, ×290. C. Exothecial cells, ×290. D. Leaves, ×22. E. Habit, ×9. F. Stomate, ×290. G. Peristome, ×80. H. Upper cells, ×290.

TYPE: U.S.A. Colorado, Gilpin Co.: 5 mi. E of Corona Pass on Corona Pass Rd., *Shaw 2628* (Holotype: MICH; Isotype: J. Shaw). Paratypes: Colorado, Garfield Co: 30 mi. N of Glenwood Springs, *Hermann 24272* (COLO). Washington, Pierce Co.: Mt. Rainier Nat. P., above Paradise Pt., *Shaw 2453* (J. Shaw).

Moist snowmelt areas in the alpine zone. Colorado, Utah, Wyoming, Washington. Map 7.

The var. *seriata* differs from the var. *bolanderi* in its luxuriant growth and extremely pale leaves often arranged more or less distinctly in vertical rows. At their extremes, the two varieties are very distinct, although several collections

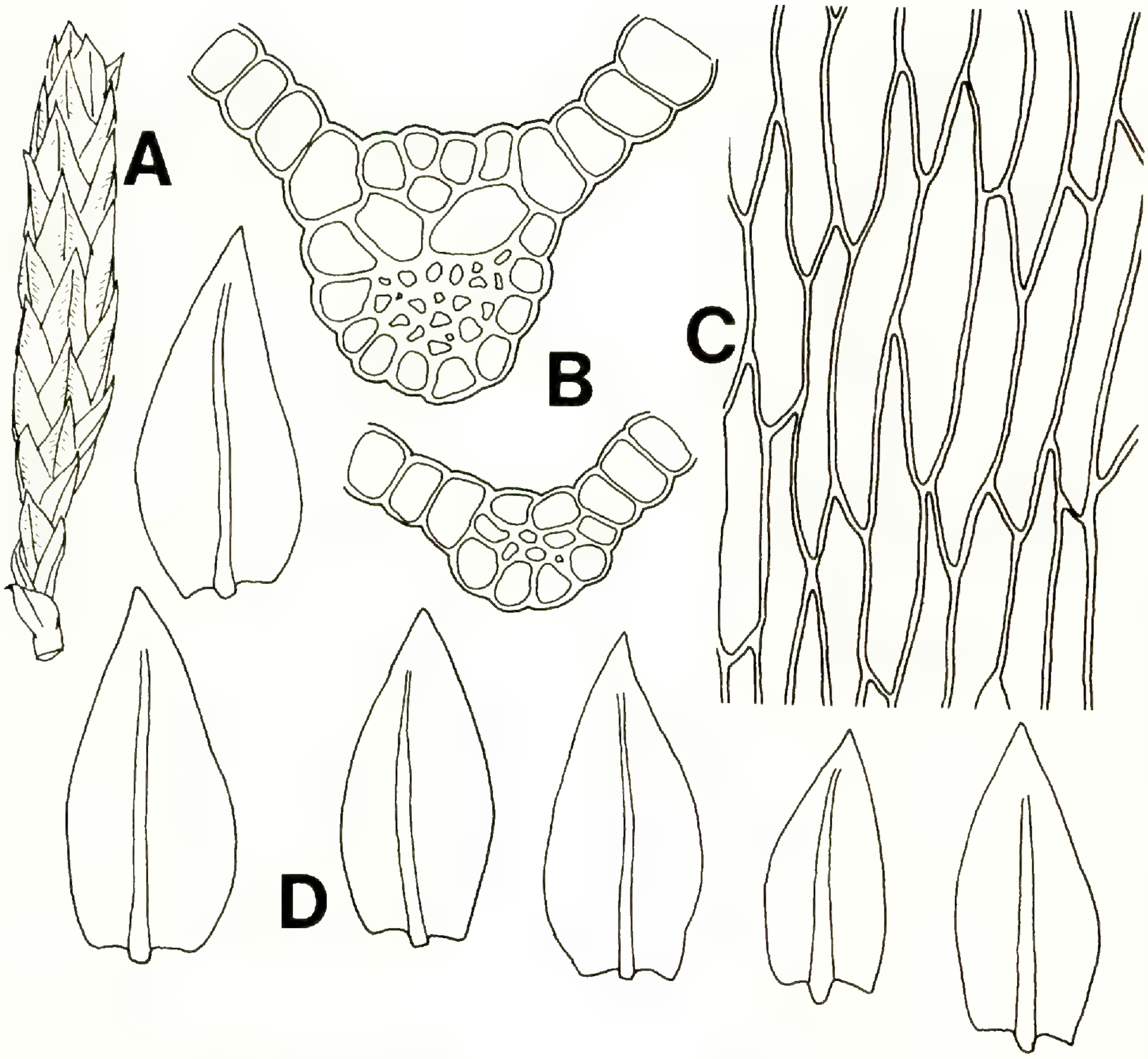


FIG. 9. *Pohlia bolanderi* var. *seriata*. A. Habit, ×35. B. Costae, transverse sections near the leaf base (above) and apex (below), ×290. C. Upper leaf cells, ×290. D. Leaves, ×35.

show intergradation (e.g. *Shaw 2448*, ALTA; *Lawton 2833*, WTU). When well developed, the var. *seriata* looks much like *Conostomum tetragonum* (Hedw.) Lindb. Whereas the var. *bolanderi* is often fertile, I have seen only one specimen of the var. *seriata* with sporophytes (Utah, Cache Co., *Behling 288*, NY). One other collection (*Shaw 2678*, ALTA) has female inflorescences, but all other specimens seen are completely sterile.

Geographic ranges of the two varieties are different, though overlapping (Map 7). The var. *seriata* is characteristic of lush snowmelt areas whereas the var. *bolanderi* grows most frequently on rather dry tundra soil.

7. **Pohlia longicollis** (Hedw.) Lindb., Musci Scand. 18. 1879.

Webera longicollis Hedw., Spec. Musc. 169. 41. f. 1–5. 1801. (Lectotype: G: Hedw.–Schwaegr.).

Bryum longicolle (Hedw.) Sw., Monthl. Rev. 34: 538. 1801.

Hypnum longicolle (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3. 1803.

Webera alpina Hoppe & Hornsch. *ex* Hornsch., Flora 2: 104. 1819. (Lectotype: GZU–Hoppe; Isotype: G: Hedw–Schwaegr.).

Bryum grimsulanum Brid., Bryol. Univ. 1: 628. 1826. (Lectotype: B–Brid.; Isotype: G: Hedw.–Schwaegr.).

Mnium crudum var. *longicolle* (Hedw.) Wahlenb., Fl. Suec. 2: 725. 1826.

Webera grimsulana (Brid.) Brid., Bryol. Univ. 2: 829. 1827.

Bryum hornschuchii Spreng., Syst. Veg. 4: 212. 1827 (*nom. illeg. incl. sp. prior.—W. alpina, W. grimsulana*).

Webera longicollis var. *alpina* (Hoppe & Hornsch. *ex* Hornsch.) Fuernr., Flora 12(Ergbl. 2): 36. 1829.

W. longicollis var. *grimsulana* (Brid.) Fuernr., Flora 12(Ergbl. 2): 36. 1829.

Bryum elongatum var. *alpinum* (Hoppe & Hornsch. *ex* Hornsch.) B. & S. *in* B. S. G., Bryol. Eur. 4: 102. 1839.

Pohlia clavata Sendtn., Flora 23: 61. 1840 (*hom. illeg.*; Lectotype: M).

Bryum lucidum Jam. *in* Durand, J. Ac. Nat. Sc. Philadelphia ser. 2, 3: 202. 1856. (Lectotype: FH).

Lamprophyllum longicolle (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 26. 1871.

Bryum nitens Kindb., Bih. K. Svensk. Vet. Ak. 7: 66. 1883 (*hom. illeg.*; Lectotype: S–Kindb.).

B. elongatum ssp. *longicolle* (Hedw.) Kindb., Bih. K. Svensk Vet. Ak. Handl. 7: 66. 1883.

B. nitescens Kindb., Bot. Not. 196 (based on *B. nitens*).

Webera pennina De Not. *ex* Par., Ind. Bryol. 1353. 1898 (*nom. nud. in synon.*—*W. longicollis*).

W. elongata var. *alpina* (Hoppe & Hornsch. *ex* Hornsch.) Herib., Mem. Ac. Sc. Clermont-Ferrand ser. 2, 14: 310. 1899.

Pohlia longicollis var. *alpina* (Hoppe & Hornsch. *ex* Hornsch.) Williams, Bull. New York Bot. Gard. 2: 364. 1902.

Webera nitescens (Kindb.) Kindb. *ex* Macoun, Cat. Canad. Pl. 7: 246. 1902.

Pohlia longicollis var. *grimsulana* (Brid.) Amann, Fl. Mousse. Suisse 2: 179. 1919.

Robust, shiny green plants frequently forming small populations in rock crevices. Stems 8–30 mm, generally simple though sometimes forking. Leaves erect to erect-spreading, crowded and imbricate, lanceolate, acute to acuminate, 1.5–2.6 mm long, coarsely serrate near the apices; upper cells linear rhomboidal, 80–140 μm long, 6–9 μm wide, thin-walled. Paroicous; perichaetial bracts gradually differentiated from lower leaves, to 3.8 mm. Capsules inclined 10°–90° from vertical, elongate-cylindric, 4–6 mm long; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, blunt to acute; exostome teeth yellow to brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ⅓–½ the exostome length; segments keeled but narrowly perforate; cilia short, rarely long. Spores 16–23 μm, distinctly roughened. Fig. 10.

Soil of roadbanks and streambanks, frequently in rock crevices with *P. crudoides* at high latitudes. Circumboreal; across northern North America south in the Rockies to Colorado and in the Appalachians to Tennessee and North Carolina; absent from the Cascade-Sierra Nevada systems. Japan; India; recently reported from East Africa (Mt. Kenya). Map 8.

Exsiccati: Bauer, Musci Eur. Exs. 908 as *W. longicolla* (BH, COLO); Drummond, Musci Amer. 270 as *B. elongatum* (CANM, MICH, NY); Grout, N. Am. Musci Perf. 398 as *P. elongata* (CAS, COLO); Hartmann, Bryac. Scand. Exs. 164 as *W. longicolla* (BH, COLO); Mougeot & Nestler, Stirpes Crypt. 1409 as *W. longicolla* (BH, CANM); Rabenhorst, Bryoth. Eur. 359 as *W. longicolla* (NY, UC), 873 as *W. longicolla* (NY).

Characterized by its large size, glossy, crowded leaves, and paroicous inflorescences, *P. longicollis* is strikingly beautiful. Like *P. elongata* and *P. bolanderi*, *P. longicollis* has the endostome segments narrowly (or scarcely) perforate.

8. **Pohlia polycarpa** (Mitt.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

Bryum polycarpum Mitt., Linn. Soc. Bot. 12: 293. 1869. (Lectotype: NY).

Webera polycarpa (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 134. 1875.

Bryum aggregatum C. Müll., Bull. Herb. Boiss. 5: 181. 1897. (Lectotype: BM–Hampe).

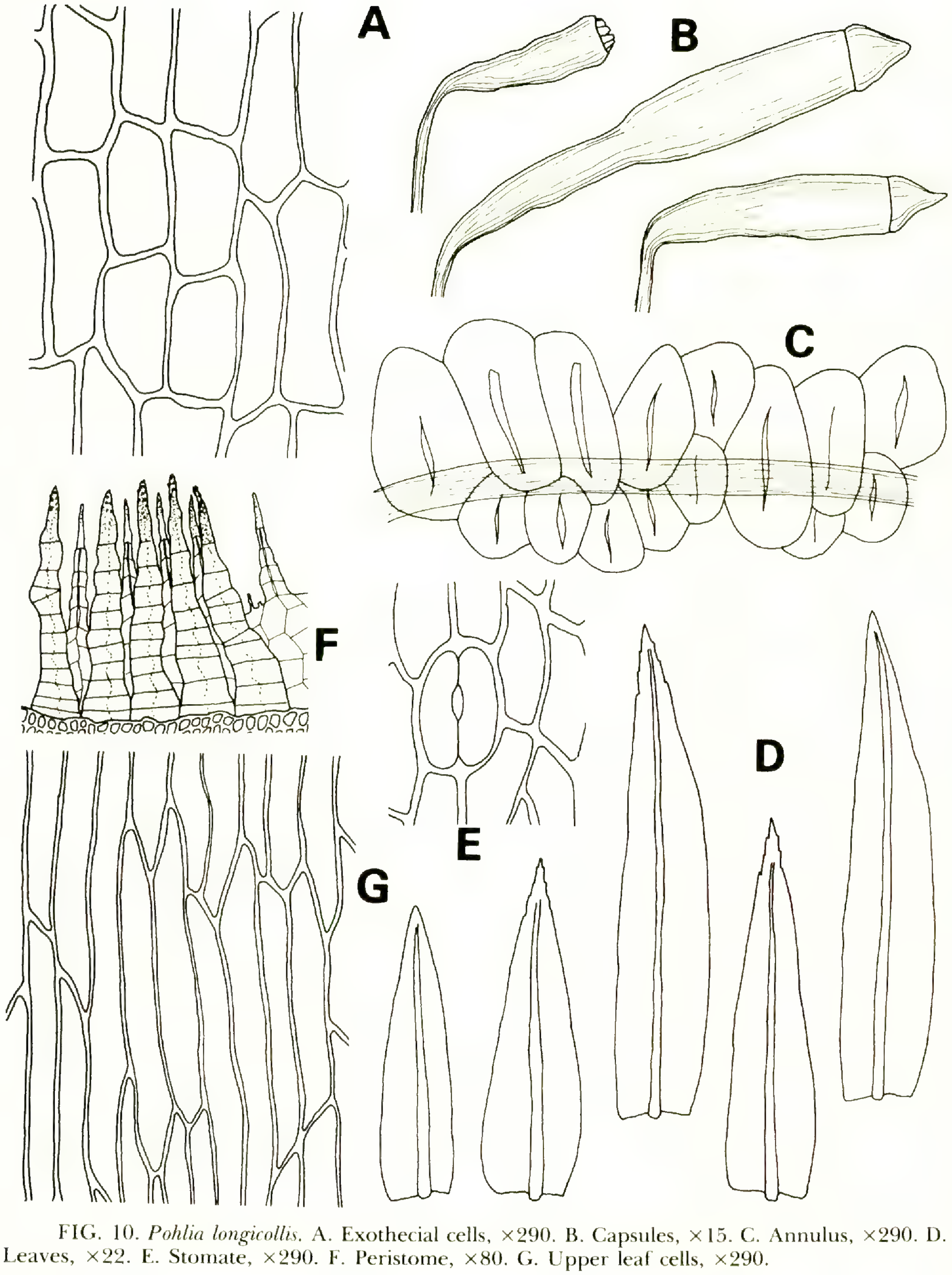


FIG. 10. *Pohlia longicollis*. A. Exothecial cells, ×290. B. Capsules, ×15. C. Annulus, ×290. D. Leaves, ×22. E. Stomate, ×290. F. Peristome, ×80. G. Upper leaf cells, ×290.

Webera aggregata (C. Müll.) Par., Ind. Bryol. 1343. 1898.

Pohlia aggregata (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

P. pluriseta Herz., Beih. Bot. Centralbl. 26: 71. 14. 1910. (Lectotype: JE).

Slender to tiny, glossy green plants forming low turfs. Stems 3–10 mm high, generally simple when sterile, branching by 1–3 innovations below the perichaetia, simple or with a subfloral innovation when bearing perigonia. Leaves erect to erect-spreading, crowded and imbricate, lanceolate, 0.7–1.4 mm long, serrate to serrulate at the apices; upper cells linear-rhomboidal, 50–95 μm long,

thin-walled. Dioicous; perichaetial leaves lanceolate to linear-lanceolate, scarcely differentiated or gradually longer than the lower leaves, to 2.5 mm; perigonial bracts shortly acute, erect to erect-spreading. Capsules inclined 10°–95° from vertical, narrowly cylindric, 2.5–4 mm long, 1–4 per perichaetium; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula convex to conic, apiculate; exostome teeth yellow-brown to brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline to very pale yellow; basal membrane ca. ⅓ the exostome length; segments weakly to strongly keeled, not or scarcely perforate; cilia rudimentary to absent. Spores 16–20 μm, very finely roughened. Fig. 11.

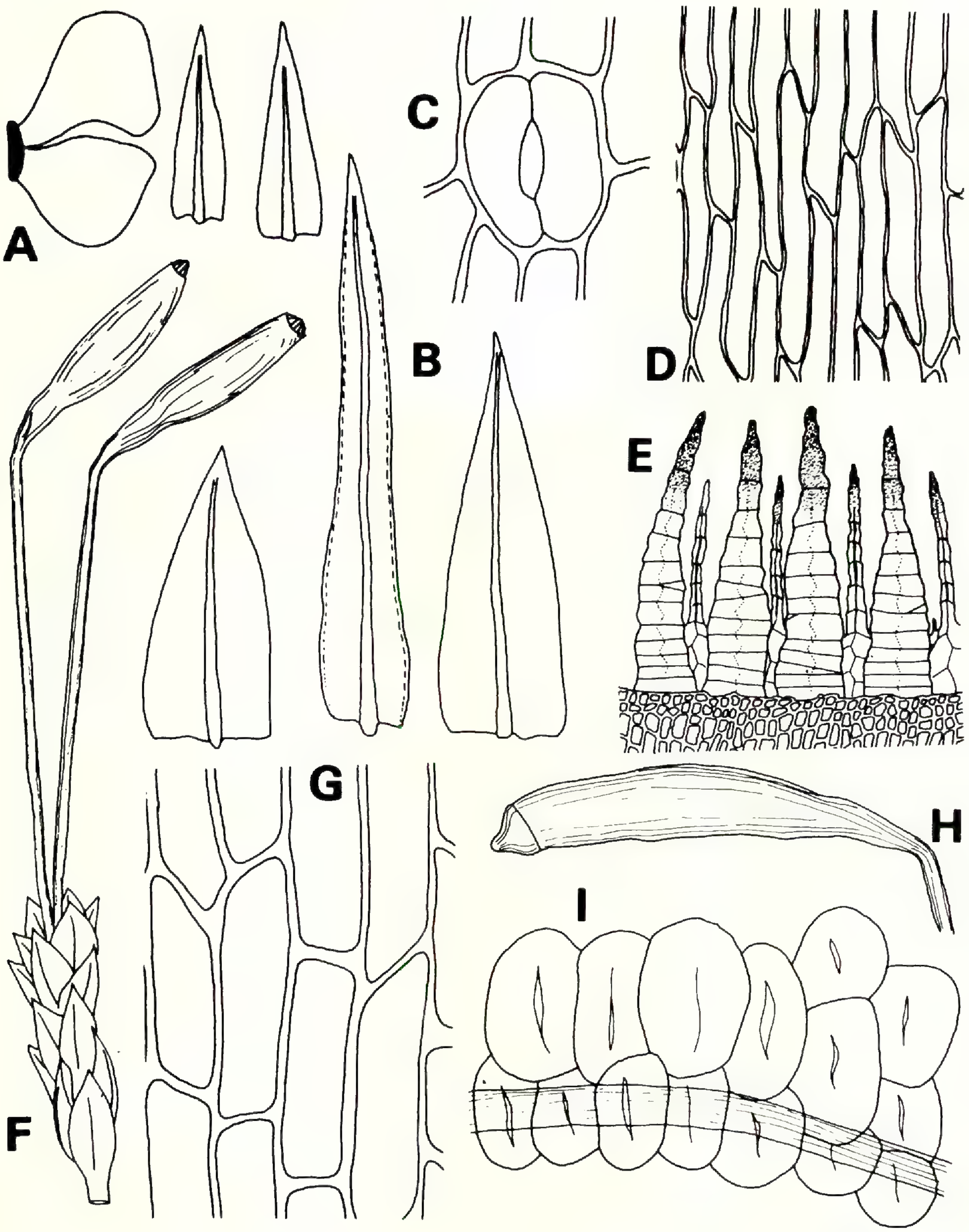


FIG. 11. *Pohlia polycarpa*. A. Lateral view of annular cells, ×290. B. Leaves, including a long perichaetial bract with recurved margins, ×22. C. Stomate, ×290. D. Upper leaf cells, ×290. E. Peristome, ×80. F. Habit, ×8. G. Exothecial cells, ×290. H. Capsule, ×15. I. Annulus, ×290.

On alpine soil; Guatemala (Volcán del Fuego—type, Tajumulco); Bolivia; Peru, Chile. Map 9.

An Andean species, *P. polycarpa* is known in Central America from only two localities in Guatemala. Distinguished at once from related species by the polysetous condition, *P. polycarpa* is otherwise very similar to the northern *P. bolanderi*. *Webera costesii* Card. & Thér. is synonymous with *P. polycarpa* according to a note in the New York Botanical Garden written by Thériot.

9. **Pohlia obtusifolia** (Brid.) L. Koch, Leafl. West. Bot. 6: 20. 1950.
Bryum obtusifolium Brid., Musc. Rec. 2(3): 52. 1803 (type not seen).
Bryum cucullatum Schwaegr., Spec. Musc. Suppl. 1(2): 94. 68. 1816.
Pohlia cucullata (Schwaegr.) Bruch *ex* Hochstetter, Flora 1: 274. 1826.
Bryum vogesiacum Dub. *in* Cand., Bot. Gall. 2: 552. 1830. (Lectotype: RO).
Webera cucullata (Schwaegr.) Schimp., Coroll. 66. 1856.
W. cucullata var. *hausmannii* De Not., Atti Univ. Genova 1: 430. 1869. (Lectotype: RO).
Lamprophyllum cucullatm (Schwaegr.) Lindb., Act. Soc. Sc. Fenn. 10: 87. 1871.
Pohlia cucullata (Schwaegr.) Lindb., Musci Scand. 19. 1879.
Webera microcaulon C. Müll. & Kindb. *in* Macoun, Cat. Canad. Pl. 6: 114. 1892. (Lectotype: S–Kindb.).
W. polymorphoides Kindb. *in* Macoun, Cat. Canad. Pl. 6: 111. 1892. (Lectotype: S–Kindb.).
Pohlia polymorphoides (Kindb. *in* Macoun) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.
Bryum obrutum Stirt. *ex* Dix., J. Bot. 61: 71. 1923 (*nom. nud. in synon.—P. cucullata*).
Bryum oxoniense Dix., Bryol. 32: 2. 1929. (Lectotype BM–Dix; Isotype: BH).
Pohlia serrulata Bruch *ex* Podp., Consp. 337. 1954 (*nom. nud. in synon.—P. cucullata*).

Very small to elongate, pale-green to blackish, rather dull plants in low to deep turfs. Stems 3–8(–25) mm high, simple or rarely forking when sterile, simple or rarely with 1–4 innovations when fertile. Leaves spreading to erect, crowded to distant, broadly lanceolate, broadly acute, subtly cucullate, 0.7–1.4 mm long, serrulate to serrate at the apices; upper cells broadly rhombic, 30–55(–70) μm long, 12–16(–20) μm wide, lax and thin-walled. Paroicous; perichaetial bracts scarcely to moderately differentiated, to 2.8 mm long. Capsules 160°–180° from vertical, broadly pyriform, 2.0–3.5 mm long; exothecial cells elongate-rectangular, 40–75 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula blunt or umbonate, rarely acute-conic; exostome teeth slenderly triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane low, up to ⅓ the exostome length; segments ± keeled but narrow and delicate, rather broadly perforate; cilia rudimentary to absent. Spores 17–25 μm, distinctly roughened. Fig. 12.

On soil, typically in the alpine zone, frequent in moist, rich snowmelt areas. Circumboreal; in North America known from Alaska, Yukon Territory, Northwest Territories, British Columbia, Alberta, Washington, California, Montana, Wyoming, Colorado, Utah, Labrador, Newfoundland, Quebec, Vermont; India; Japan. Map 10.

Exsiccati: Bauer, Musci Eur. et Amer. Exs. 1925 as *P. cucullata* (CANM), Musci Eur. exs. 312 as *P. cucullata* (BH); Erbar, Crittogam Ital. 1012 as *W. cucullata* (NY, UC); Husnot, Musci Gall. 462 as *W. ludwigii* (BH, NY); Lisowski, Bryoth. Polon. 613 as *P. cucullata* (CANM); Macoun, Can. Musci 468 as *W. cucullata* (NY), 636 a *W. polymorphoides* (NY); Mougeot & Nestler, Stirpes Cryptog. 830 as *P. cucullata* (CANM, NY); Rabenhorst, Bryoth. Eur. 442 as *W. cucullata* (NY); 1215 as *W. ludwigii* (NY);

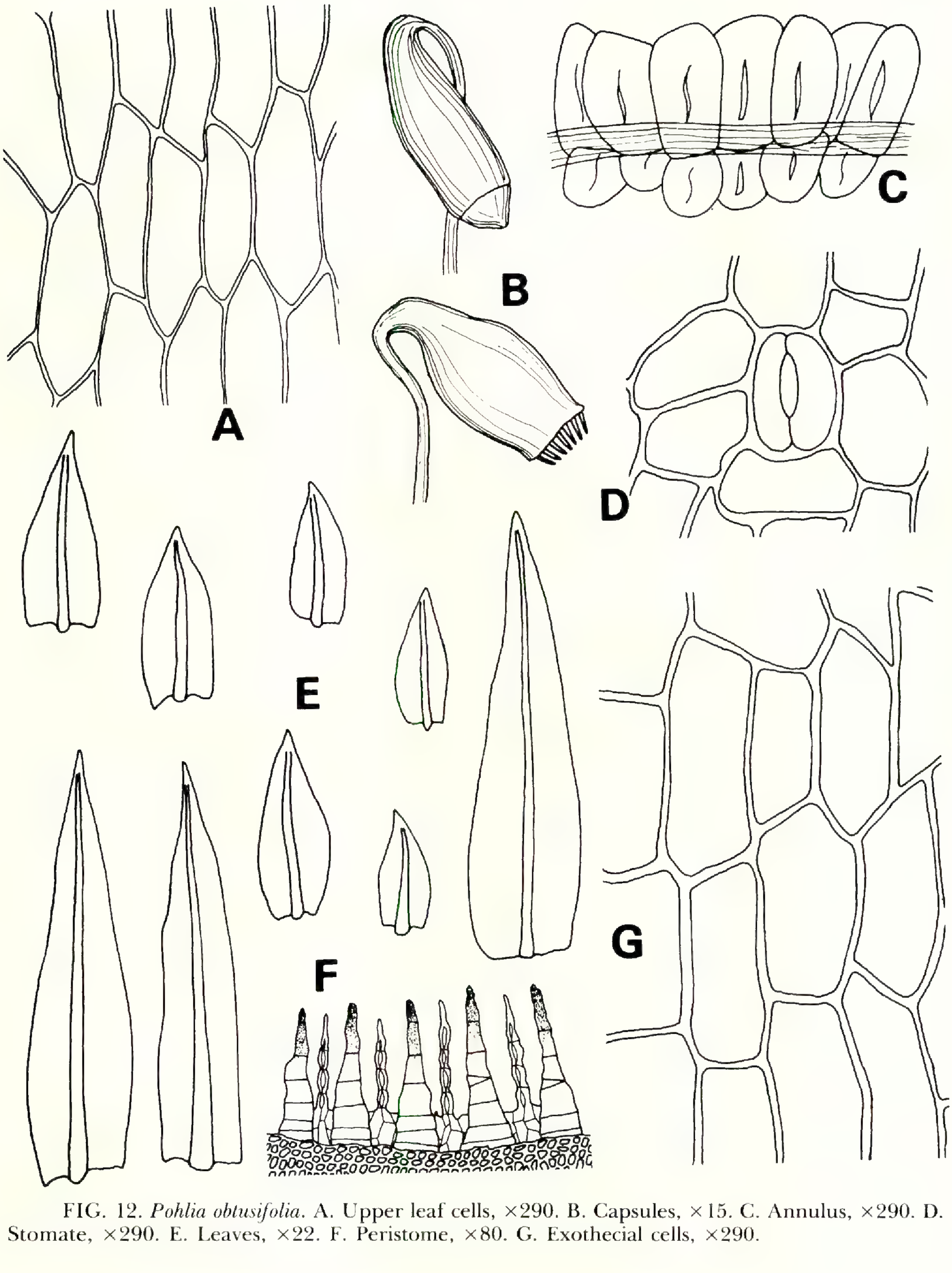


FIG. 12. *Pohlia obtusifolia*. A. Upper leaf cells, ×290. B. Capsules, ×15. C. Annulus, ×290. D. Stomate, ×290. E. Leaves, ×22. F. Peristome, ×80. G. Exothecial cells, ×290.

Sull. & Lesq., Musci Bor. Am. (ed. 1) 176 as *B. cucullatum* (MICH, NY), (ed. 2) 265 as *B. cucullatum* (BH, MICH, NY).

Pohlia obtusifolia is readily distinguished from other species by a combination of gametophytic and sporophytic attributes: paroicous inflorescence, lax, thin-walled leaf cells, and the delicate endostome segments which, although poorly developed, are broadly perforate.

Fruiting plants are typically very small (3–6 mm high), but sterile forms growing in unusually moist sites can reach 2–4 cm. Such forms rarely even produce gametangia, and are most reliably identified by the subtly cucullate

leaves and broad cells (12–13 μm or more wide). It is characteristic of elongate expressions to be almost black except for the apical few leaves which are pale-green.

Pohlia obtusifolia is not obviously related to any other North or Central American *Pohlia*. The non-sinuose exothecial cells and revoluble annuli indicate a possible relationship to the previous eight species, but the endostome is more similar to that of *P. cardotii*.

In spite of extensive inquiries to European and North American herbaria, I have been unable to typify *P. obtusifolia*. However, I accept the name rather than using the slightly later *P. cucullata* primarily because after Schwaegrichen described *Bryum cucullatum* in 1816, he noted (1830) that his species was synonymous with Bridel's *Bryum obtusifolium*. Unfortunately, there is no specimen of *B. obtusifolium* in Schwaegrichen's herbarium.

10. **Pohlia crudoides** (Sull. & Lesq.) Broth. *in* Engler & Prantl, Nat Pfl. 1(3): 548. 1903.

Bryum crudoides Sull. & Lesq., Proc. Am. Ac. Arts & Sc. 4: 278. 1859. (Isotype: NY–Mitt.).

Webera crudoides (Sull. & Lesq.) Jaeg., Ber. S. Gall. Naturw. Ges. 1877–78: 440. 1879.

Pohlia crassinervis Lindb., Bot. Centralb. 6: 363. 1881. (Lectotype: H–SOL).

P. crassidens Lindb., Rev. Bryol. 10: 5. 1883. (Lectotype: H–SOL).

Webera trachydontea San., Bot. Centralbl. 13: 247. 1883. (Lectotype: H–SOL).

Bryum crassidens (Lindb.) Kindb., Bih. K. Svensk. Vet. Ak. Handl. 7: 66. 1883.

Webera crassidens (Lindb.) Kindb., Forh. Vid. Selsk. Christiania 1886: 22. 1888.

W. crassinervis (Lindb.) Par., Ind. Bryol. 1343. 1898.

Bryum trachydonteum (San.) C. Müll., Gen. Musc. Fr. 220. 1901.

Medium size to robust, somewhat glossy plants frequently forming small populations in rock crevices. Stems 4–10(–25) mm, deep cherry-red, generally simple but sometimes forking near the base when sterile. Leaves erect-spreading to erect, rather distant, narrowly or rarely broadly lanceolate, acute, 1.0–2.2 (–2.6) mm long, serrate to serrulate at the apices; with strongly recurved margins; upper cells linear-hexagonal, 35–60(–85) μm long, with thin walls. Dioicous; perichaetial bracts lanceolate to linear lanceolate, to 3 mm long; perigonial bracts shortly to longly acuminate, erect to erect-spreading. Capsules inclined 30°–90° from vertical, ovoid-cylindrical, 2.5–4 mm long; exothecial cells shortly to longly rectangular, 30–80 μm long, with straight to weakly sinuose walls; stomates superficial; annuli of 2–3 cell rows, revoluble or separating irregularly; opercula convex to conic, acutely to bluntly apiculate; exostome teeth whitish to yellow, slenderly triangular, rounded at the apex, coarsely papillose throughout, scarcely bordered, weakly trabeculate; endostome whitish to hyaline; segments narrow and scarcely keeled, very narrowly perforate to entire; basal membrane low, to ⅓ the exostome length; cilia absent or rarely rudimentary. Spores 15–25 μm, finely roughened. Fig. 13.

On soil especially in rock crevices in tundra habitats; according to Ochi (1959), on soil also in the deciduous zone of Japan (as var. *revolvens*). Alaska, Yukon Territory, Northwest Territories and British Columbia; Greenland; northern Europe and Asia; Japan; India. Map 11.

Exsiccati: Noguchi, Musci Jap. 936 as *P. crudoides* (CANM, NY); Savicz-Lubitzkaja, Hep. et Musci U.R.S.S. Exs. 96 as *P.crudoides* (CANM, CAS).

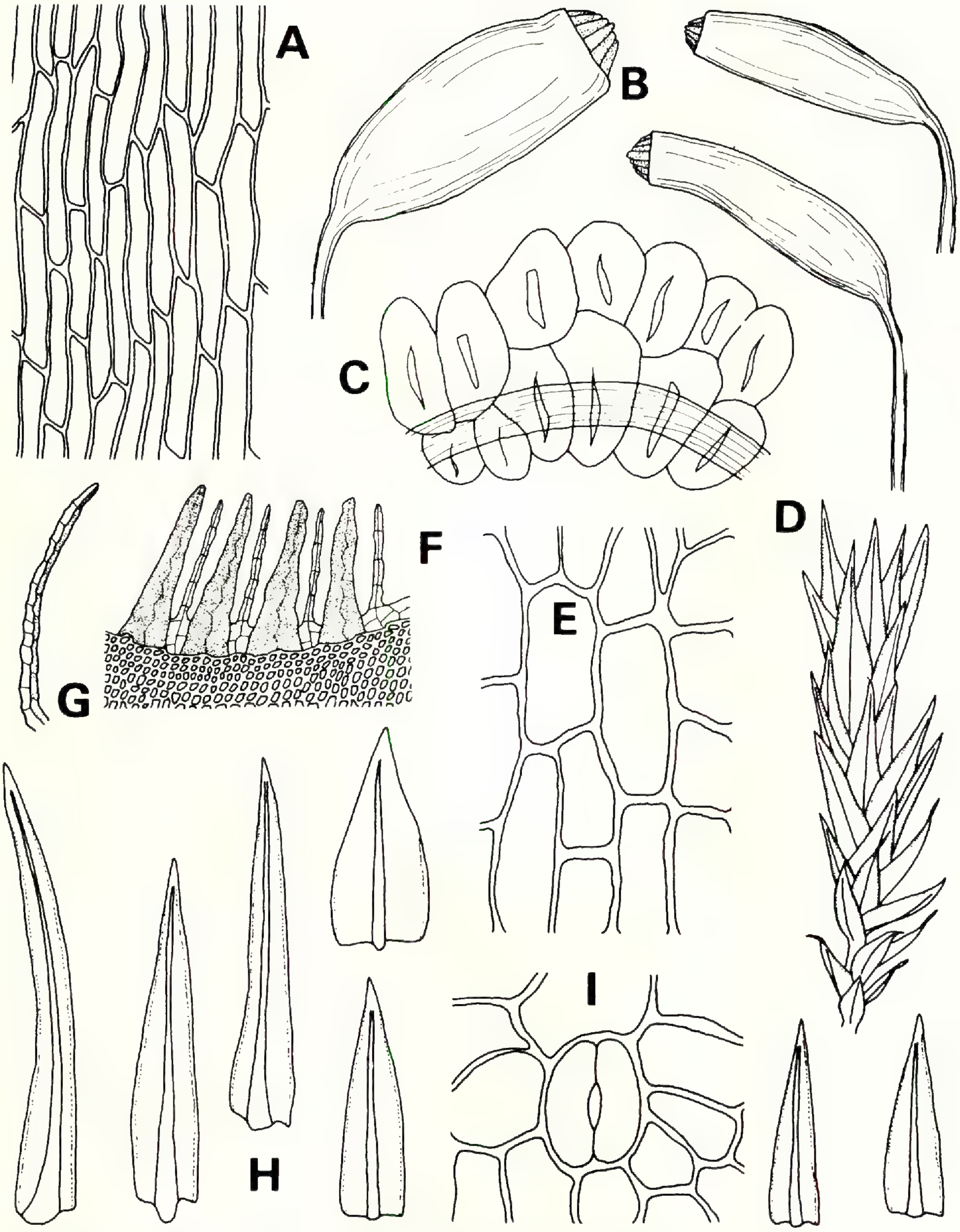


FIG. 13. *Pohlia crudoides*. A. Upper leaf cells, ×290. B. Capsules, ×15. C. Annulus, ×290. D. Habit, ×4. E. Exothecial cells, ×290. F. Peristome, ×80. G. Lateral view of exostome tooth showing weakly developed trabecula, ×80. H. Leaves, perichaetial bracts on the leaf, ×22. I. Stomate, ×290.

Pohlia crudoides can be recognized by cherry-red stems and obviously recurved leaf margins. The leaves are generally long, narrow and somewhat stiff, although I have seen a few sterile plants from the Yukon Territory with broader, less stiff leaves and hardly recurved margins. *Pohlia crassinervis* Lindb. typifies such expressions, which do not seem to justify separation.

Pohlia crassidens Lindb. and *Webera trachydontea* San. are based on the same type specimen (collected in Opdal by Kaurin). There is no specimen representing *W. trachydontea* in the Sanio herbarium (Rusińka *in litt*, 1979). To avoid future ambiguity, I have chosen a single specimen in Lindberg's herbarium to

lectotypify both names. The Himalayan type of *Webera timmioides* Broth. is close to *P. crudoides*, distinguishable solely by its very robust stature. Both syntypes lack sporophytes.

11. **Pohlia papillosa** (C. Müll. *ex* Jaeg.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Bryum papillosum C. Müll., Syn. 1: 326. 1848. (Lectotype: NY; Isotype BM–Besch.). *hom. illeg.—non B. papillosum* Dicks.

B. tenellum Schimp. *ex* C. Müll., Syn. 2: 572. 1851. (Lectotype: BM–Schimp.; Isotype: NY).

Brachymenium tenellum (Schimp. *ex* C. Müll.) Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 195. 1872.

B. papillosum (C. Müll. *ex* Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 122. 1875.

B. subglobosum Schimp. *ex* Besch., Ann. Sci. Nat. Bot. ser. 6, 3: 204. 1876. (Lectotype: BM–Besch.; Isosyntype: NY, BM–Hampe).

Bryum mammillosum C. Müll., Bull. Herb. Boiss. 5: 550. 1897. (Lectotype: NY).

Brachymenium mammillosum (C. Müll.) Par., Ind. Bryol. Suppl. 39. 1900.

Pohlia mammillosa (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Pohlia subglobosa (Schimp. *ex* Besch.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Webera papillosa (C. Müll. *ex* Jaeg.) Herz., Biblioth. Bot. 87: 79. 1916.

W. mammillosa (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 362. 1924.

W. subglobosa (Schimp. *ex* Besch.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 362. 1924.

Medium-sized dull green plants sometimes forming extensive turfs. Stems 5–25 mm, simple or commonly forking when sterile, with 1–4 innovations below the perichaetia, simple when bearing perigonia. Leaves erect-spreading, frequently distant on sterile stems, crowded when fertile, lanceolate, 0.7–1.4 mm long, serrate to serrulate at the apices; upper cells rhomboidal, 60–90(–110) μm long, 6–9 μm wide, with firm walls. Gemmae numerous in the upper leaf axils, arising in clusters in each axil, linear-vermicular, oblong, or obconic, 100–250 μm long but apparently indeterminate in growth, brown or whitish, pink or reddish, with 1–4 peglike, erect, leaf primordia at the apex, the primordia sometimes 2–3 cells broad at the base. Dioicous; perichaetial bracts linear-lanceolate, to 3.0 mm long; perigonial bracts erect-spreading. Capsules inclined 10°–100° from vertical, broadly to narrowly pyriform, narrowed at the mouth, sometimes curved and slightly asymmetric, 2.5–4.0 mm long; exothecial cells isodiametric to shortly rectangular, 35–60 μm long, with straight or rarely sinuose, often strongly bulging walls; stomates superficial to somewhat sunken; annuli of 1(2) cell rows, separating irregularly; opercula convex and apiculate or shortly and bluntly rostrate (and sometimes curved upward); exostome teeth whitish to yellow, ± fused near the base; slenderly triangular, ± blunt at the apices, coarsely papillose throughout, scarcely bordered, weakly trabeculate; endostome whitish to hyaline, papillose; segments narrow and scarcely keeled, very narrowly perforate to entire; basal membrane low, to ⅓ the exostome length; cilia absent or rarely rudimentary. Spores 17–21 μm, finely roughened. Fig. 14–15.

On soil of roadbanks or in other disturbed sites, most frequent at moderate altitudes in cloud forests; Mexico (Chiapas, Chihuahua, Hidalgo, Mexico, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Veracruz); Cuba; Dominican Republic; Haiti; Jamaica; Guatemala; Costa Rica; Panama; Columbia, Venezuela; Peru; Ecuador; Brazil. Map 12.

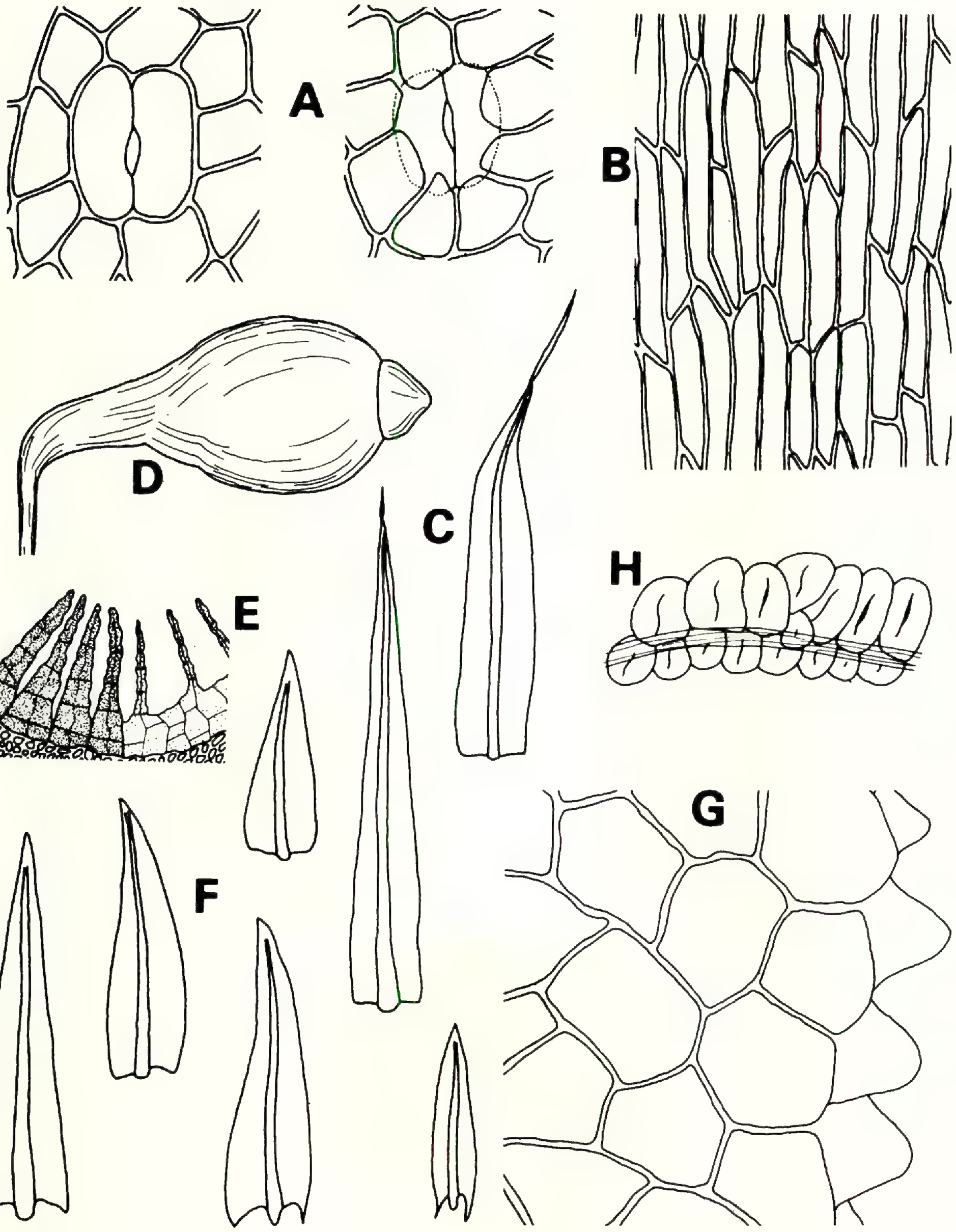


FIG. 14. *Pohlia papillosa*. A. Stomates, ×290. B. Upper leaf cells, ×290. C. Perichaetial bracts, ×22. D. Capsule, ×15. E. Peristome, ×80. F. Leaves, ×22. G. Exothecial cells, ×290. H. Annulus, ×290.

Exsicatti: Pringle, Plantae Mex. 10635 as *W. didymodontia* (MO).

Ecologically, *P. papillosa* replaces *P. annotina* and related species in the Neotropics. It reproduces by axillary gemmae, and is common in disturbed areas. The gemmae are variable in shape, encompassing most of the forms characteristic of *P. proligera* and *P. annotina* combined. They are usually very small (ca. 100 μm) and linear-vermicular with one primordium, but are sometimes obconic with 2–4 peglike (or rarely more or less laminate) primordia. Many specimens have only dense clusters of small vermicular gemmae. Several Mexican collections have very small ovoid gemmae with poorly developed leaf primordia

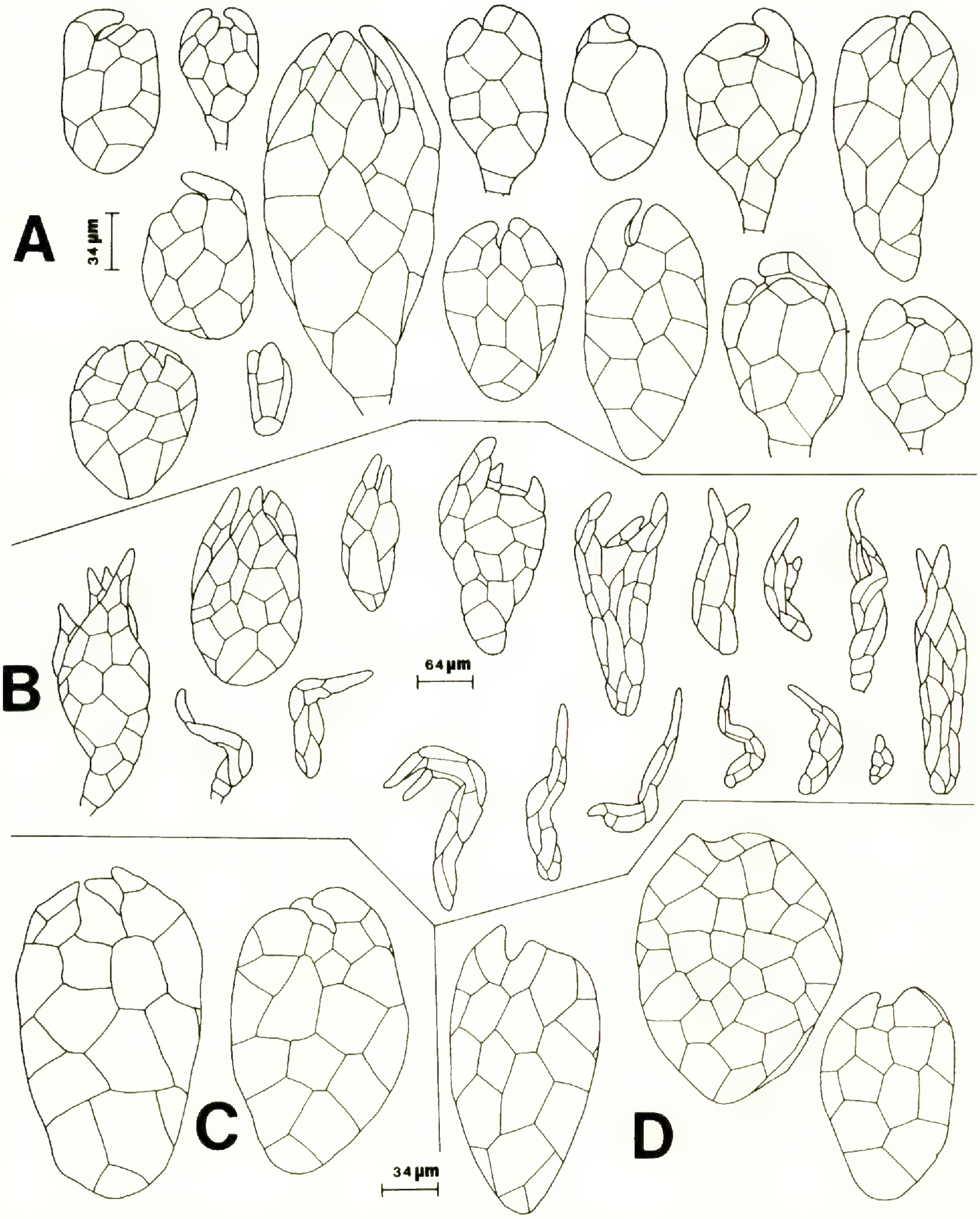


FIG. 15. Gemmae of *Pohlia* and *Bryum* species. A. *Pohlia richardsii*. B. *Pohlia papillosa*. C. *Bryum* sp., *Fife 2827*. D. *Bryum gemmiluscens* Wilz. & Dem., *Dehle*, 1824 (BM).

(e.g. *Bowers et al. 5385; Sharp et al. 1325; Iwatsuki & Sharp 5339b;* all in TENN). These may prove to be poor examples of *P. papillosa*, but require further study.

Contrary to Andrews (1950), I find *P. papillosa* to be consistently distinct from the Old World, *P. flexuosa* Hook. The two are quite similar, but *P. flexuosa* has longly acuminate exostome teeth (370–600 µm vs 240–370 µm in *P. papillosa*), completely separate to the base and segments distinctly keeled and narrowly perforate. The exothecial cells are often only weakly bulging whereas they are strongly so in *P. papillosa*. Gemmae of *P. flexuosa* are often scarce, but are generally linear-obconic to ovoid with 3–5 peglike primordia. I have seen *P. flexuosa* from Japan, the Philippines, China, India, Nepal and Africa (Rwanda), and it is apparently endemic to the Old World.

A number of species have been segregated from *P. flexuosa* on the basis of differences in gemmae form. Andrews (1950) referred *Pohlia delicatula* (Mitt.) Broth. to the synonymy of *P. flexuosa*, but it is a clearly distinct species distinguished by leaf shape and aereolation as well as gemmae morphology. Like the European *P. muyldermansii* Wilz. & Dem., *P. delicatula* has two kinds of gemmae: linear with poorly developed primordia and tiny, isodiametric to ovoid types. Unlike *P. muyldermansii*, the ovoid gemmae do not have protruding walls. The Hawaiian *P. leucostomoides* (Broth.) Bartr. has larger, translucent ovoid gemmae devoid of primordia in the leaf axils.

12. **Pohlia richardsii** Shaw, sp. nov.

Plantae caespitosae vel gregariae. Caules fertiles ramosissimi, breves, steriles plerumque simplices, gemmiferi duplo et triplo longiores, uniformiter foliosi, erecti. Folia lanceolata vel lineali-lanceolata, apice irregulariter serrata, inferne margine reflexa, areolis cellulis superioribus linearibus. Capsulae late pyriformes. Gemmae abundantes, axillis foliorum summorum, intense rubrae, ovoideae.

Dull green plants. Stems 5–15 mm, simple when sterile or bearing antheridia, innovating rather abundantly when bearing archegonia. Leaves erect-spreading to spreading when moist, scarcely altered on drying; 0.7–1.4 mm long, 0.3–0.6 mm wide, lanceolate, acute, somewhat decurrent by 3–4 rows of rectangular cells; margins plane to ± reflexed, serrate to serrulate near the apex or halfway to the base, entire below; costa ending 1–3 cells below the apex; upper cells linear-rhomboidal, (40–)50–80(–95) μm long, 6–9 μm wide, thin- to firm-walled, not or rarely vermicular, undifferentiated along the margin, rectangular near the base. Gemmae numerous to few in upper leaf axils, arising in clusters in each axil, rarely appearing single on older shoots, spheroidal, ovoid, obovoid, or obconic, about 110–160 μm long but apparently indeterminate in growth, deep red to orange-red, with 1–4 short, inconspicuous leaf primordia at the apex, the primordia rarely rudimentary, sometimes peglike, but mostly laminate (3 cells or more broad at the base), incurved over the apex, paler than the body but not green. Dioicous; perigonia bulbiform; outer bracts longly acute to acuminate, erect to erect-spreading from an erect base; perichaetia terminal, rather inconspicuous; outer bracts to ca. 2.2 mm long, triangular- to linear-lanceolate; margins recurved from base to apex. Sporophytes uncommon; setae 10–15 mm high, orange to orange-red; capsules inclined about 90°, 2.5–3.5 mm long, tan to brown, broadly pyriform, abruptly contracted to a well-developed neck; exothecial cells isodiametric to short-rectangular, 35–55 μm long, 18–40 μm wide, with non sinuose but bulging walls; stomates superficial to ± sunken, 35–55 μm long; annuli of 1(2) cell row(s), separating irregularly; opercula bluntly convex to hemispheric; exostome teeth white to yellowish-white, narrowly lanceolate, ± blunt, (200–)220–330(–370) μm long, weakly bordered, hardly trabeculate, densely and rather coarsely papillose from apex to base dorsally; endostome white to hyaline; basal membrane ca. ⅓ the exostome length; segments linear to linear-laneolate, not or slightly keeled, not perforate; cilia none. Spores 10–20 μm, finely papillose to nearly smooth. Fig. 15–16.

TYPE: Costa Rica, Volcán Poas, on banks of volcanic ash near edge of water, c. 2,500 m, 20 Feb. 1965, *Richards R 6010* (Holotype: MICH). Paratypes: Colombia, Dept. Santander: Vicinity of California, 3000 m, *Kilip & Smith* (NY). Dept. Cundinamarca: ca. 1 km S of Usme, ca. 9000 ft., *King et al. C–6000* (US). Ecuador, Prov. Napo: Páramo de Guamami, N of Quito-Baeza Rd., 4200 m, *Steere E–250* (NY). Venezuela, Nova Granada, *Linding* (NY).

On soil. Costa Rica (De Alajuela, San José); Colombia; Venezuela; Ecuador. Recently collected in the Dominican Republic (La Vega, *Shaw 5621*). Map 13.

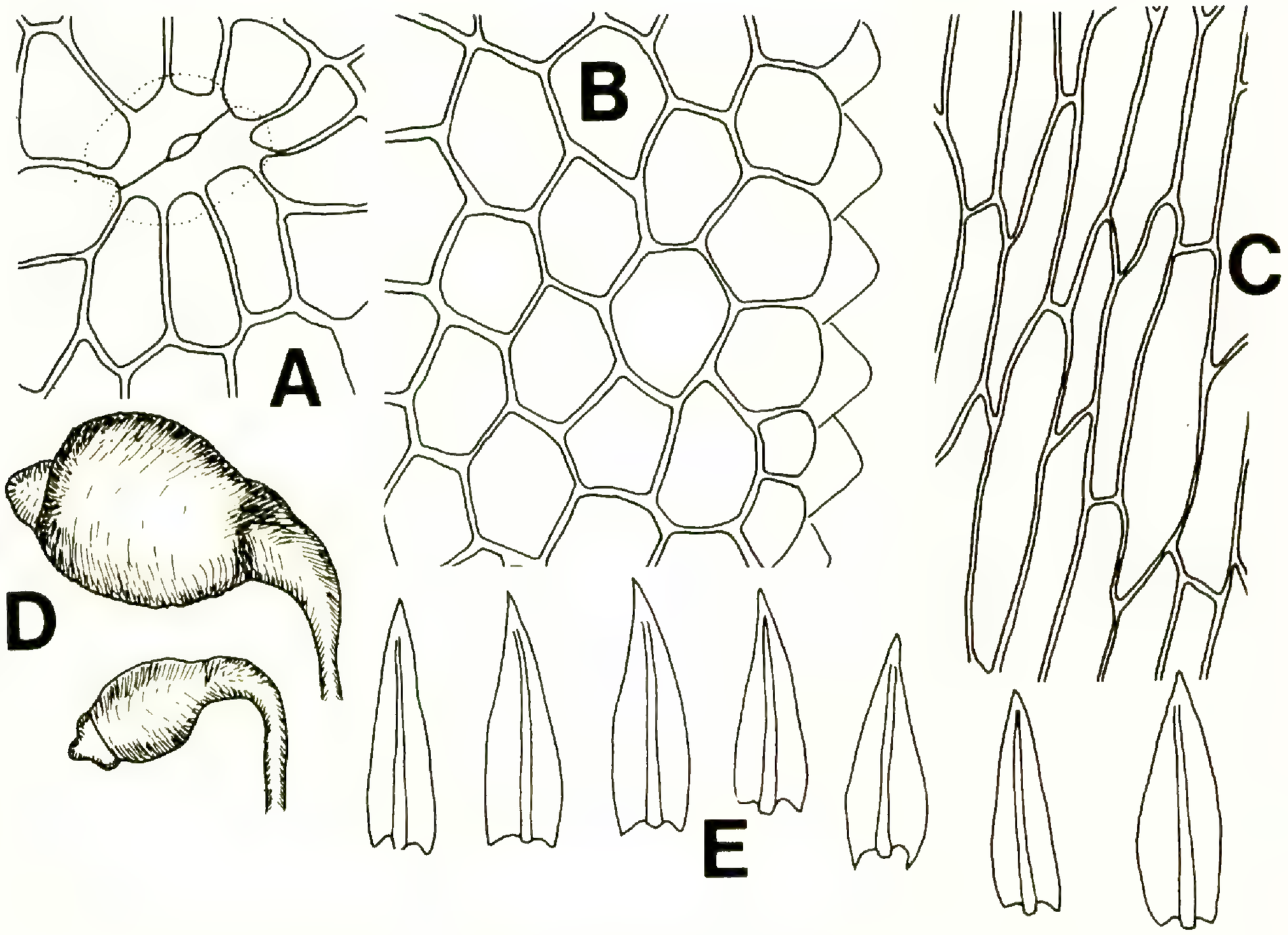


FIG. 16. *Pohlia richardsii*. A. Stomate, ×290. B. Exothecial cells, ×290. C. Upper leaf cells, ×290. D. Capsules, ×15. E. Leaves, ×22.

Pohlia richardsii was collected by Paul Richards in 1965 and was subsequently sent to H. Crum, who recognized it as a new species. I am grateful to them for permission to describe it here.

This is apparently a species of the nothern Andes and Central America, penetrating northward only to Costa Rica, though disjunct in the Dominican Republic. The only fruiting plants of *P. richardsii* available, all collected by D. Griffin and collaborators in Costa Rica, are unfortunatly mixed with *P. papillosa*. I was able to convince myself that at least some of the sporophytes belong to *P. richardsii* gametophytes, although there is nothing to distinguish the capsules from those of *P. papillosa*. This similarity is comparable to the uniformity among capsules of *P. annotina* and related species.

Pohlia richardsii is distinguished from *P. papillosa* by the deep red to orange, spherical to short-oblong gemmae. The only time that *P. papillosa* approaches *P. richardsii* in gemmae form is in very poorly-developed expressions of the former that have few, small gemmae, with rudimentary primordia. In such cases, the gemmae are pale, rather than dark and translucent. Even in mixed specimens of *P. papillosa* and *P. richardsii*, it is possible to separate stems of the two. *Pohlia richardsii* can also be distinguished from such other propaguliferous species as *P. pseudo-barbula* and *Pseudopohlia didymodontia* by smaller gemmae.

Gemmae like those of *P. richardsii* are found in several unrelated species of Bryaceae. For example, *Bryum gemmilucens* Wilz. & Dem. has gemmae practically indistinguishable from those of *P. richardsii* (Fig. 15). Similar forms occur on stems of a sterile and unidentified *Bryum* collected by A. Fife in Newfoundland (Fig. 15), and those of *P. andrewsii* are also similar (Fig. 23).

13. **Pohlia pseudo-barbula** (Thér.) Crum *ex* Shaw, comb. nov.

Webera pseudo-barbula Thér., Smiths. Misc. Coll. 85: 28. 17. 1931. (Lectotype: PC; Isosyntype: F).

Slender dull-green plants. Stems 5–15 mm, generally unbranched when sterile, with 1–4 innovations below the perichaetia, simple when bearing perigonia. Leaves erect to erect-spreading, crowded on the stem, lanceolate, 0.7–1.4 mm long, serrate or serrulate to midleaf or below; upper cells rhomboidal, 50–75(–90) μm long (longer on perichaetial leaves) 6–9 μm wide, with firm walls. Propagula present in clusters in upper leaf axils, ovoid to spherical or obconic, abruptly narrowed to a uniseriate stalk, red to orange, (140–)160–230(–300) μm long, with 2–5 apical and subapical, erect or incurved leaf primordia, the primordia laminate in form (2–5 cells broad at the base). Dioicous; perichaetial bracts lanceolate to linear-lanceolate, to 3.0 mm long; perigonial bracts shortly to longly acuminate, erect-spreading. Capsules inclined 10°–90° from vertical, narrowly pyriform to cylindrical, 2.5–4.0 mm long, slightly curved and asymmetric; exothecial cells longly to shortly rectangular, 35–65 μm long, with somewhat sinuose walls; stomates superficial; annuli of 2 cell rows, separating irregularly; opercula conic, acute or apiculate; exostome hyaline to whitish, narrowly triangular, ± blunt, coarsely papillose in the upper ½, more finely roughened below, scarcely bordered, weakly trabeculate; endostome hyaline; basal membrane low, to ⅓ the exostome length; segments linear but slightly keeled, not or very narrowly perforate; cilia absent or rarely rudimentary. Spores 13–20 μm, nearly smooth or somewhat roughened. Fig. 17.

On soil, especially along roadsides in montane Oak-Pine forests. Apparently endemic to Mexico, where it is known from the volcanic region around Mexico City (Distrito Federal, Hidalgo, Michoacán, Puebla). Map 14.

This species is related to *P. papillosa*, as indicated by the weakly bordered and trabeculate, rather short exostome teeth, linear scarcely keeled, narrowly split segments, and low basal membrane, lacking cilia altogether. Like *P. papillosa*, it reproduces by axillary gemmae. It is distinguished by narrowly cylindrical capsules with rectangular, nonbulging exothecial cells, and far less coarsely papillose exostome teeth that are almost smooth below.

I have examined all four of the syntypes cited by Thériot. The lectotype is an abundant specimen bearing both sporophytes and axillary gemmae. An additional specimen collected by Brother Amable in Cuautzin (no. 1827) was reported by Thériot (1932). A duplicate in the Mitten collection (NY) agrees precisely with the syntypes. Crum (1951) made the combination *Pohlia pseudobarbula* in his thesis, but since that is not considered effective publication, the combination is validated here. The author citation should therefore be *P. pseudobarbula* (Thér.) Crum *ex* Shaw.

14. **Pohlia ludwigii** (Schwaegr.) Broth., Act. Soc. Sc. Fenn. 19: 27. 1892.

Leskea ludwigii [Spreng. *ex*] Web. & Mohr, Ind. Musc. Pl. Crypt. 3: 1803. (*nom. nud.*).

Bryum ludwigii Schwaegr., Spec. Musc. Suppl. 1(2): 95. 68. 1816. (Lectotype: G: Hedw.–Schwaegr.).

Webera ludwigii (Schwaegr.) Fuernr., Flora 12(Ergbl. 2): 35. 1829.

Bryum bigelovii Sull., Rep. Expl. Surv. Rout. Railr. 4: 187. 5. 1856. (Lectotype: FH).

Webera breidleri Jur., Verh. Zool. Bot. Ges. Wien 20: 167. 3b. 1870. (Lectotype: W).

Bryum breidleri (Jur.) Hobk., Grevillea 1: 157. 1873.

Webera bigelovii (Sull.) Lesq. & James, Man. N. Am. Moss. 223. 1884.

Pohlia bigelovii (Sull.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 50. 1903.

Webera ludwigii var. *breidleri* (Jur.) Roth, Eur. Laubm. 2: 26. 1904.

Bryum grande (Kindb.) Par., Ind. Bryol. ed. 2, 1: 217. 1904 (*nom. inval. in synon.—B. ludwigii*).

Mniobryum bigelovii (Sull.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

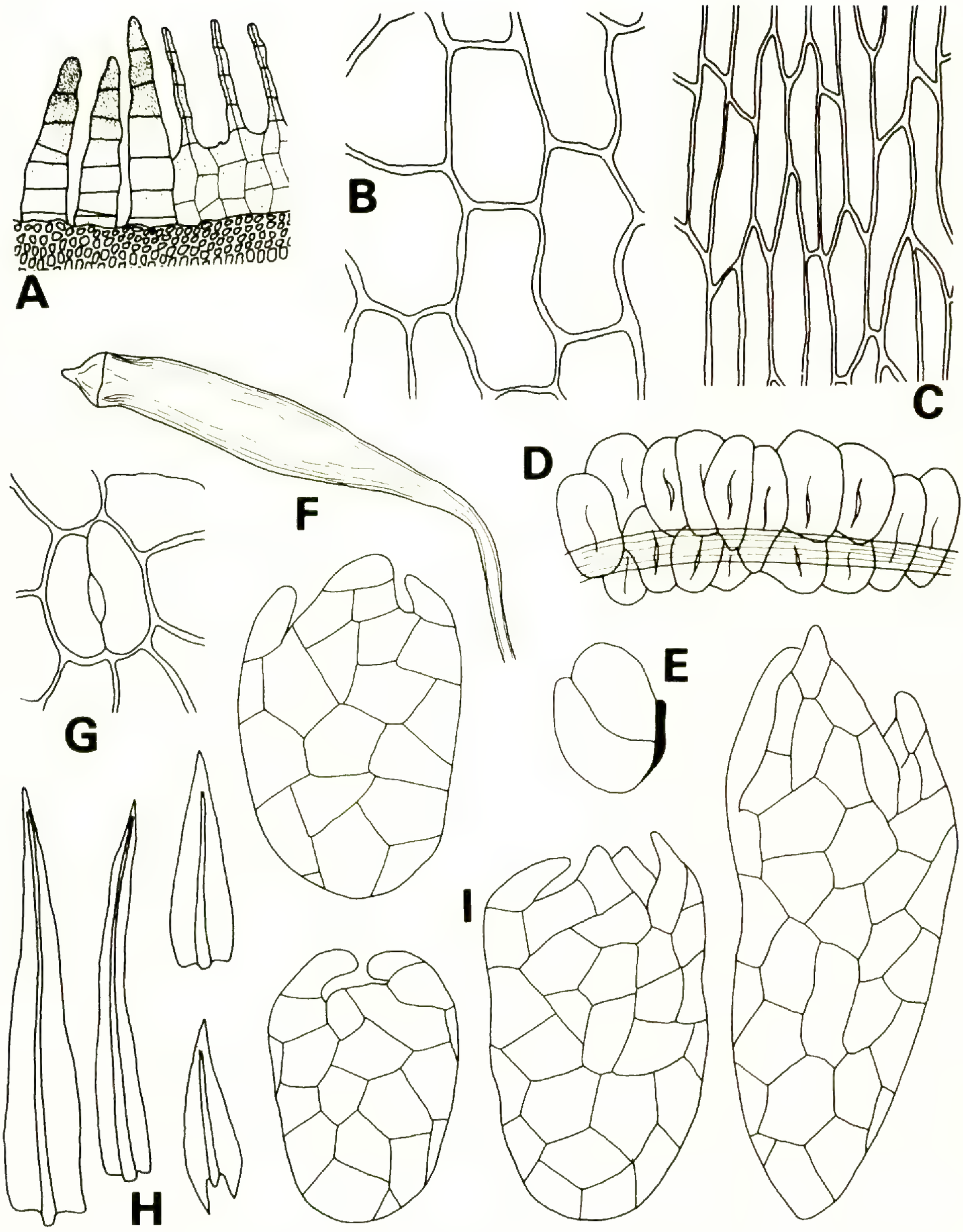


FIG. 17. *Pohlia pseudo-barbula*. A. Peristome, ×80. B. Exothecial cells, ×290. C. Upper leaf cells, ×290. D. Annulus, ×290. E. Lateral view of annular cells, ×290. F. Capsule, ×15. G. Stomate, ×290. H. Leaves, ×22. I. Gemmae, ×180.

M. ludwigii (Schwaegr.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

Pohlia sudetica Podp. *ex* Gyoerffy, Mag. Bot. Lapok 18: 21. 1919 (*nom. illeg. incl. spec. prior.—B. ludwigii*).

P. ludwigii var. *breidleri* (Jur.) Amann. Fl. Mouss. Suisse 2: 182. 1819.

Webera sudetica Giac., Atti Ist. Bot. Univ. Lab. Critt. Pavia Ser. 5, 4: 231. 1947 (*nom. illeg. incl. spec. prior.—B. ludwigii*).

Mostly robust, dull green plants in deep turfs. Stems 8–35 mm, simple or frequently forking when sterile, simple when bearing perichaetia, simple or with 1–3 innovations when bearing perigonia. Leaves spreading to erect-spreading,

distant to crowded, ovate-lanceolate, acute to rounded at the apices, 1.5–2.0 (–2.6) mm long, serrate near the apices, ± longly decurrent; upper cells rhombic to rhomboidal, 40–65(–85) μm long, 7–12 μm wide, with firm to rather thin walls. Dioicous; perichaetial bracts lanceolate, not strongly differentiated in shape but with the costa very broad at the base, to 3.2 mm long; perigonial bracts shortly to longly acuminate, erect-spreading. Capsules 90°–180° from vertical, broadly pyriform, 2–3.5 mm long; exothecial cells shortly rectangular, 25–65 μm long, with sinuose walls; stomata superficial; annuli of 2–3 cell rows, separating irregularly; opercula conic, blunt to apiculate; exostome yellow to brown, acute-triangular, most coarsely papillose at the apex, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled and broadly perforate; cilia long, nodulose. Spores 14–21 μm, finely roughened. Fig. 18.

Rare; on soil, especially in arctic or alpine tundra, often in lush snowmelt areas. North America (Alaska, British Columbia, Washington, Montana); northern and central Europe; Japan. Map 15.

Exsiccati: Bauer, Musci Eur. Am. Exs. 2027 as *W. ludwigii* (CANM), Musci Eur. Exs. 1624 as *P. ludwigii* (ALTA, NY), 1625 as *P. ludwigii* f. *adscendens* (ALTA, NY), 1626 as *P. ludwigii* f. *fragilis* (ALTA, NY), 1627a as *P. ludwigii* f. *aquatica* (ALTA, NY), 1627b as *P. ludwigii* f. *erecta* (NY); Husnot, Musci Gall. 520 as *W. ludwigii* v. *major* (BH); Lisowski, Bryoth. Polon. 286 as *P. ludwigii* (CANM).

Pohlia ludwigii is uncommon in North America. It is characteristic of moist, rich snowmelt areas in tundra sites, where it is usually sterile but forms rather deep cushions. Schofield and Tan collected beautiful fruiting plants in British Columbia (*74439*, UBC). According to Schofield (*in litt.*, 1980), capsules are produced late in the season, thus rarely collected. The species is recognized when sterile by the pink color of the lower leaves, and broadly lanceolate, longly decurrent leaves with the apices more or less cucullate (when moist).

Plants collected by Schnooberger (*1382*) and Moxley (1936, 1941) from Bruce Co., Ontario and distributed as *P. ludwigii* are *Bryum gemmiparum* De Not. Collections made by Bartram in Arizona and determined by Andrews as *P. commutata* (= *P. drummondii*) or *P.ludwigii* are also *B. gemmiparum*.

The type of *Bryum bigelovii* Sull. is, by default, an odd expression of *P. ludwigii*. Sporophytically it is more or less typical, but the leaves are not very decurrent and have rather lax, thin-walled cells. It represents the only record of *P. ludwigii* in California (although it is not surprising). The type of *Bryum ludwigii* ssp. *grande* Kindb. is a sterile *Philonotis*. A specimen of *P. ludwigii* in Schwaegrichen's herbarium closely matches his illustration, providing one of few instances where typification is unambiguous!

15. **Pohlia cardotii** (Ren. *in* Ren. & Card.) Broth.*in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

Webera cardotii Ren. *in* Ren. & Card., Rev. Bryol. 15: 71. 1888. (Type not seen).

Bryum commutatum ssp. *cardotii* (Ren. *in* Ren. & Card.) Kindb., Eur. N. Am. Bryin. 2: 388. 1897.

Pohlia porosa H. Lindb., Bull. Torr. Bot. Club 27: 318. 21. 1900. (Lectotype: H; Isotypes: COLO, DUKE, MICH, NY, UBC).

Bryum cardotii (Ren. *in* Ren. & Card.) Kindb. *ex* Par., Ind. Bryol. Suppl. 1900 (*nom. inval. in synon.—W. cardotii*).

Webera porosa (H. Lindb.) Par., Ind., Bryol. ed. 2, 5: 120. 1906.

Medium-sized to robust, dull green plants often forming deep turfs. Stems 3–10(–25) mm high, simple or forking when sterile, simple or rarely innovating below perichaetia, simple when bearing perigonia. Leaves erect to erect-

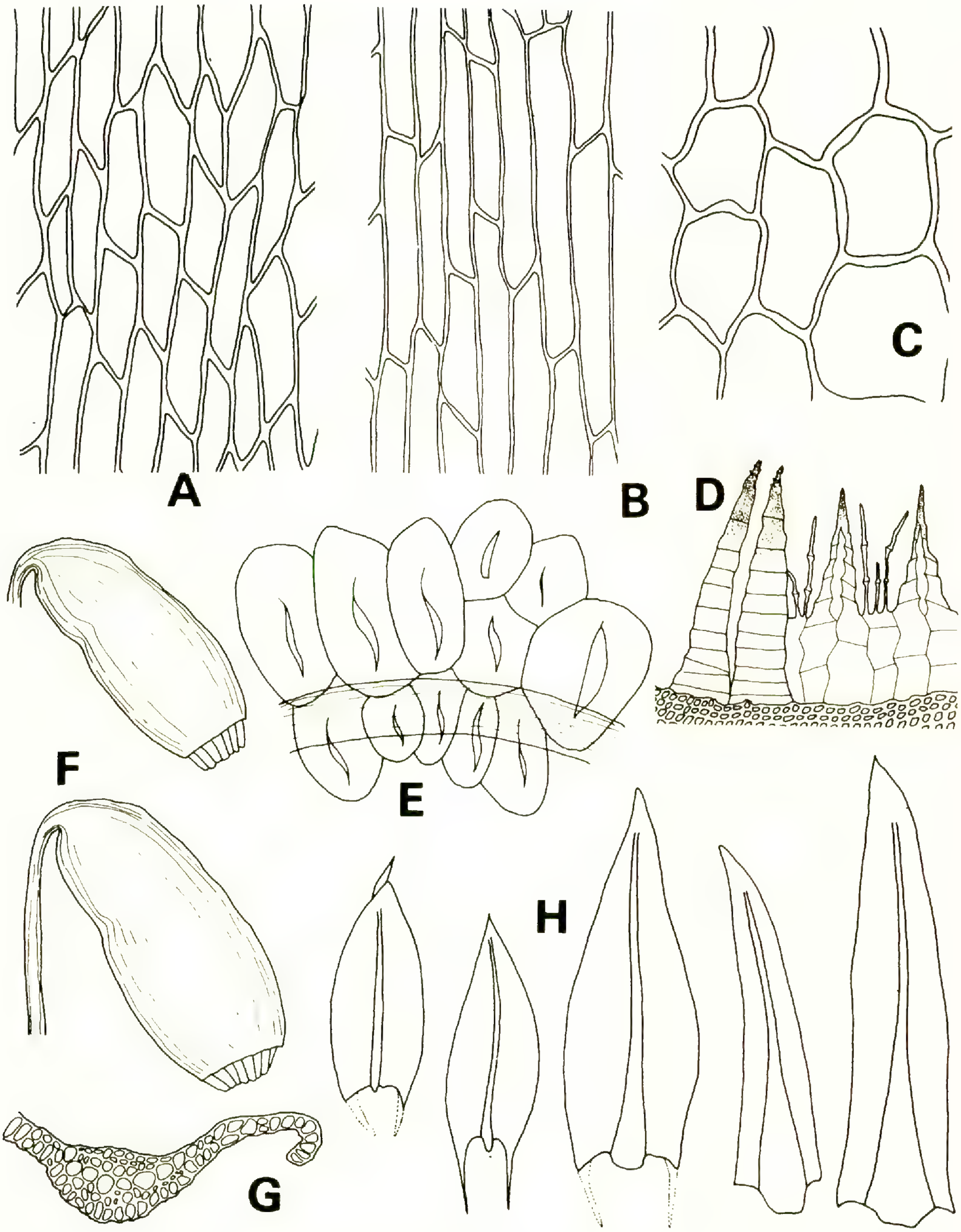


FIG. 18. *Pohlia ludwigii*. A. Upper cells of branch leaf, ×290. B. Upper cells of perichaetial bract, ×290. C. Exothecial cells, ×290. D. Peristome, ×80. E. Annulus, ×290. F. Capsules, ×15. G. Transverse section of perichaetial bract near the base, ×290. H. Leaves, ×22.

spreading, crowded, lanceolate, 0.7–1.5 mm long, serrulate to entire at the apex; costa strong, broad; upper cells rhombic, 18–35(–55) μm long, 6–9 μm wide, with thickened, often porose walls. Dioicous; perichaetial bracts somewhat differentiated, lanceolate to triangular, to 2.6 mm long; perigonial bracts shortly acute, erect. Capsules erect or nearly so, symmetric, narrowly pyriform, 2.0–3.0 mm long; exothecial cells shortly rectangular, 35–55 μm long, with ± strongly sinuose walls; stomates superficial; annuli of 2–4 cell rows, separating irregularly; opercula conic, acute; exostome teeth yellow to brown, ± narrowly triangular, obtuse or ± acute, most coarsely papillose near the apices, bordered,

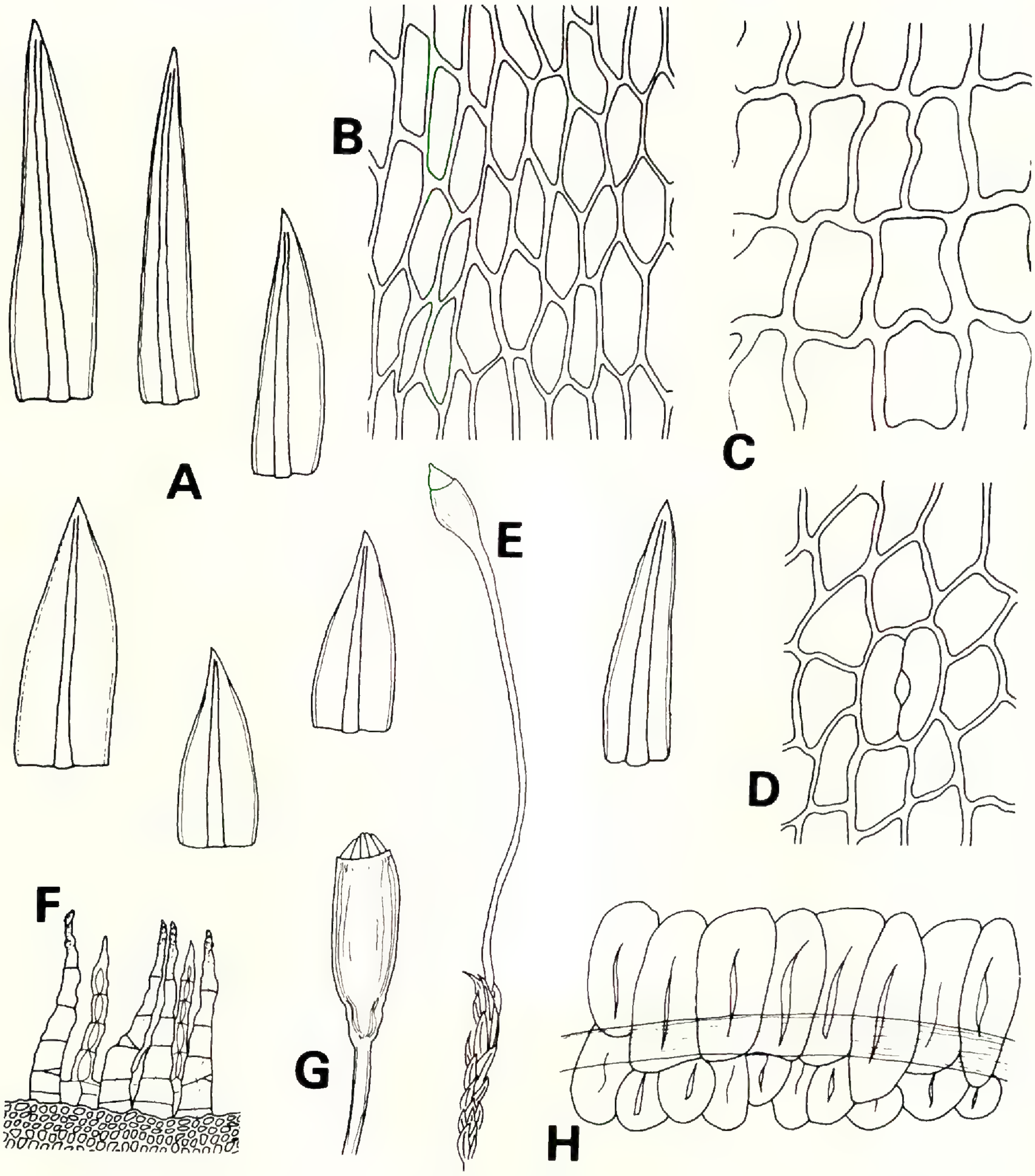


FIG. 19. *Pohlia cardotii*. A. Leaves, ×22. B. Upper leaf cells, ×290. C. Exothecial cells, ×290. D. Stomates, ×290. E. Habit, ×3. F. Peristome, ×80. G. Capsules, ×15. H. Annulus, ×290.

trabeculate; endostome hyaline; basal membrane very low, less than ⅓ the exostome length; segments narrow but somewhat keeled and broadly perforate; cilia rudimentary to lacking. Spores 14–19 μm, finely roughened. Fig. 19.

Uncommon; on soil in alpine or subalpine sites. Apparently endemic to western North America; Alaska, British Columbia, Washington and California. Map 16.

Exsiccati: Allen, Mosses of the Cascade Mts. 56 as *P. porosa* (isotypes, see above for representative herbaria).

A relatively rare alpine species, *P. cardotii* is easily recognized by the erect capsules, very low basal membrane, and especially when sterile, strongly recurved leaf margins and rather thick-walled cells. *Pohlia crudoides* is the only other American species with strongly recurved margins (except that the perichaetial bracts of most are recurved). When sterile, *P. crudoides* is distinguished by the red stems, narrower leaves and longer, thinner-walled cells. Except for one Alaskan specimen of *P. cardotii* their ranges do not overlap.

A type for *P. cardotii* could not be located in Paris. However, the distinctive nature of this species leaves little question of the application of the name. In the future, if an isotype is not found, a neotype should be selected.

16. **Pohlia erecta** Lindb., Bot. Not. 1882: 195. 1882. (Lectotype: H–SOL; Isotypes: H, O, WTU).

Mielichhoferia defecta Sanio, Bot. Centralbl. 13: 248. 1883. (Lectotype: H–SOL).

Webera defecta Sanio, Bot. Centralbl. 13: 248. 1883 (*nom. nud. in synon.—M. defecta*).

Mielichhoferia erecta (Lindb.) Kindb., Forh. Vid. Selsk. Christiana 1888(6): 22. 1888.

Webera erecta (Lindb.) Limpr., Laubm. Deutschl. 2: 239. 1891.

Pohlia defecta (Sanio) Andr. *in* Grout, Moss Fl. N. Am. 2: 189. 71. 1935.

Slender, rather glossy plants. Stems 3–8 mm, generally simple when sterile or bearing perichaetia, with 1–2 innovations when bearing perigonia. Leaves erect-spreading to erect, more or less crowded, lanceolate; 0.7–1.2 mm long, serrate to serrulate near the apex; upper cells rhomboidal, 35–60 μm long, 6–9 μm wide, thin-walled. Dioicous; perichaetial bracts slightly differentiated, to 2.2 mm long; perigonial bracts shortly acuminate, erect. Capsules erect or nearly so, symmetric, slenderly pyriform, 2.0–3.0 mm long; exothecial cells shortly rectangular, 25–60 μm long, with sinuose walls; stomates superficial; annuli of 1(2) cell row(s), separating irregularly; exostome teeth yellow to light brown, narrowly triangular, somewhat irregular, obtuse, papillose (but not coarsely so) near the apices, bordered, ± trabeculate; endostome hyaline; basal membrane very low, less than ⅓ the exostome length; segments rudimentary and irregular or ± elongate and perforate; cilia absent. Spores 15–21 μm, finely roughened. Fig. 20.

Very rare, on soil in the alpine zone. Western North America (Yukon Territory, British Columbia and Washington) and Fennoscandia. Map 17.

The erect capsules resemble those of *P. cardotii*, but the endostome of *P. erecta* is even more reduced. Sanio (1883) described this species as a *Mielichhoferia*. Although *P. erecta* seems at home in *Pohlia*, the distinctions between plants of the so-called Mielichhoferioideae (*Mielichhoferia, Synthetodontium, Haplodontium*) and *Pohlia* are sometimes ill-defined.

Pohlia erecta differs from *P. cardotii* in having soft-textured leaves with plane margins, thinner-walled cells and narrower costae.

When sterile, *P. erecta* resembles a small version of *P. drummondii*, especially in having reddish stems. Further similarities between *P. erecta* and *P. drummondii* include the aspect and branching of male plants (Fig. 20) and strongly sinuose exothecial cells. These combined probably indicate close phylogenetic affinity.

17. **Pohlia beringiensis** Shaw, sp. nov.

Plantae erectae, graciles, plerumque steriles. Caulis simplex, 4–15 mm altus. Folia pallida, erecta, imbricata, lanceolata, ad apicem serrulata, cellulis linearibus. Gemmae frequenter adsunt, oblongae, cerasinae.

Slender, pale-whitish plants diffusely scattered in small populations. Stems 4–15 mm, simple. Leaves erect, imbricate (moist or dry), 0.9–1.3 mm long, 0.3–0.6 mm wide, narrowly lanceolate, gradually acute, slightly decurrent; margins plane, serrulate near the apex, entire below; costa ending 3–5 cells below the apex; upper cells linear-rhomboidal, ± vermicular, thin-walled, 60–90(–100) μm long, 6–10 μm wide, somewhat longer and narrower along the margin. Gemmae single in 1–4 upper leaf axils, oblong-bulbiform, about 500–650(–1000) μm long, deep cherry-red when moist, red or black when dried, with 3–6 large, broadly

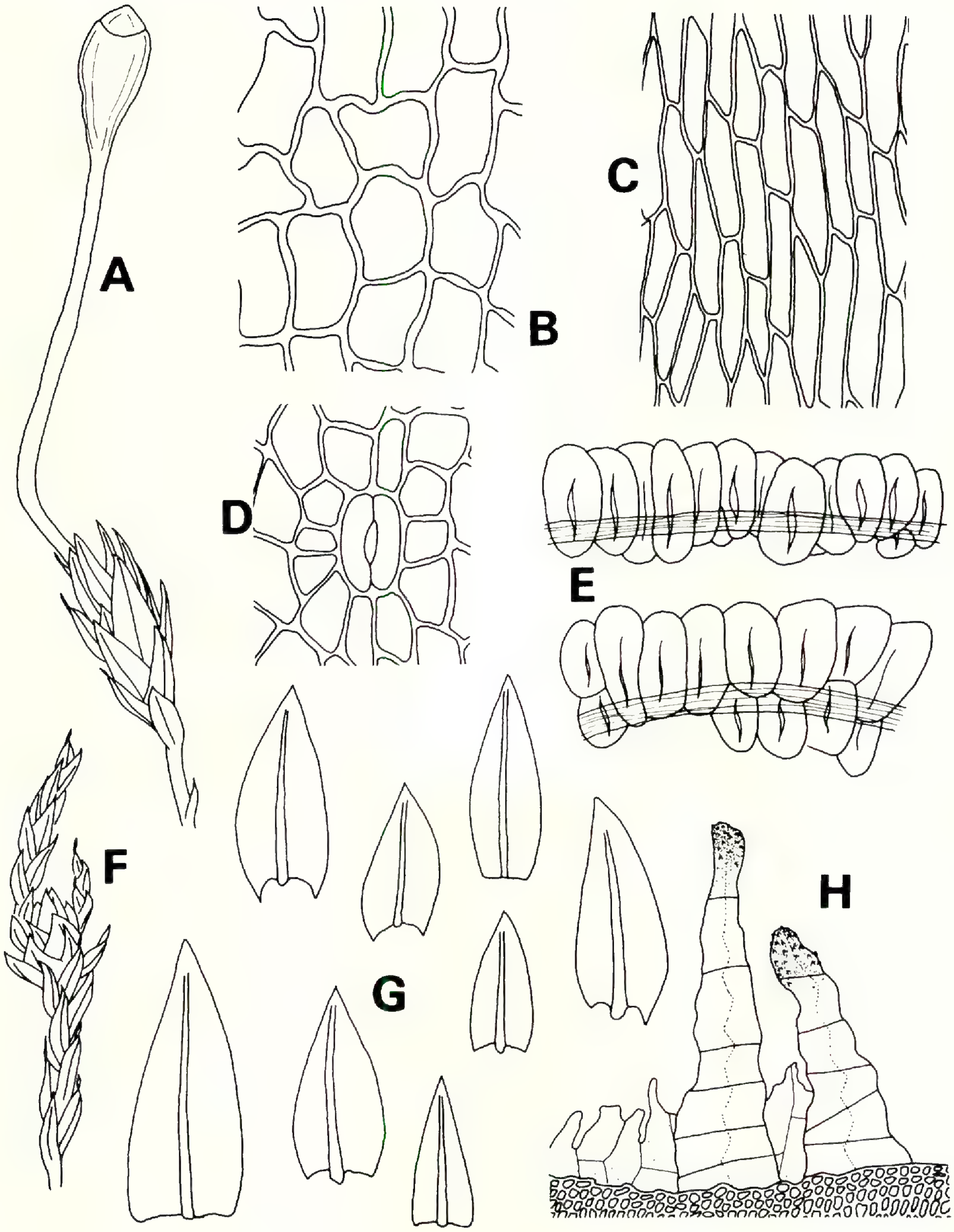


FIG. 20. *Pohlia erecta*. A. Habit, female plant, ×5. B. Exothecial cells, ×290. C. Upper leaf cells, ×290. D. Stomate, ×290. E. Annuli, ×290. F. Habit, male plant showing subfloral innovations, ×5. G. Leaves, ×22. H. Peristome, ×250.

laminate leaf primordia at the apex and frequently lower, the primordia green. Inflorescences and sporophytes unknown. Fig. 21.

TYPE: Alaska, Paxson area, 11.7 km W of Paxson on Hwy. 8., 22 July 1979, *Shaw 3794* (Holotype: MICH). Paratypes: Alaska, Honolulu area, 57.5 km S on Hwy. 3 from junction with Hwy. 8 at Cantwell, 24 July 1979, *Shaw 3889* (ALTA). Yukon Territory, Ogilvie Mts., Tombstone Mt. area, 71.3 km N of Hwy. 3 on the Dempster Hwy., 16 July 1979, *Shaw 3466* (MICH).

On organic-poor soil in mountainous areas, especially in roadside ditches. Central Asia (Altai Mts.) and northwestern North America (Alaska and Yukon Territory). Map 18.

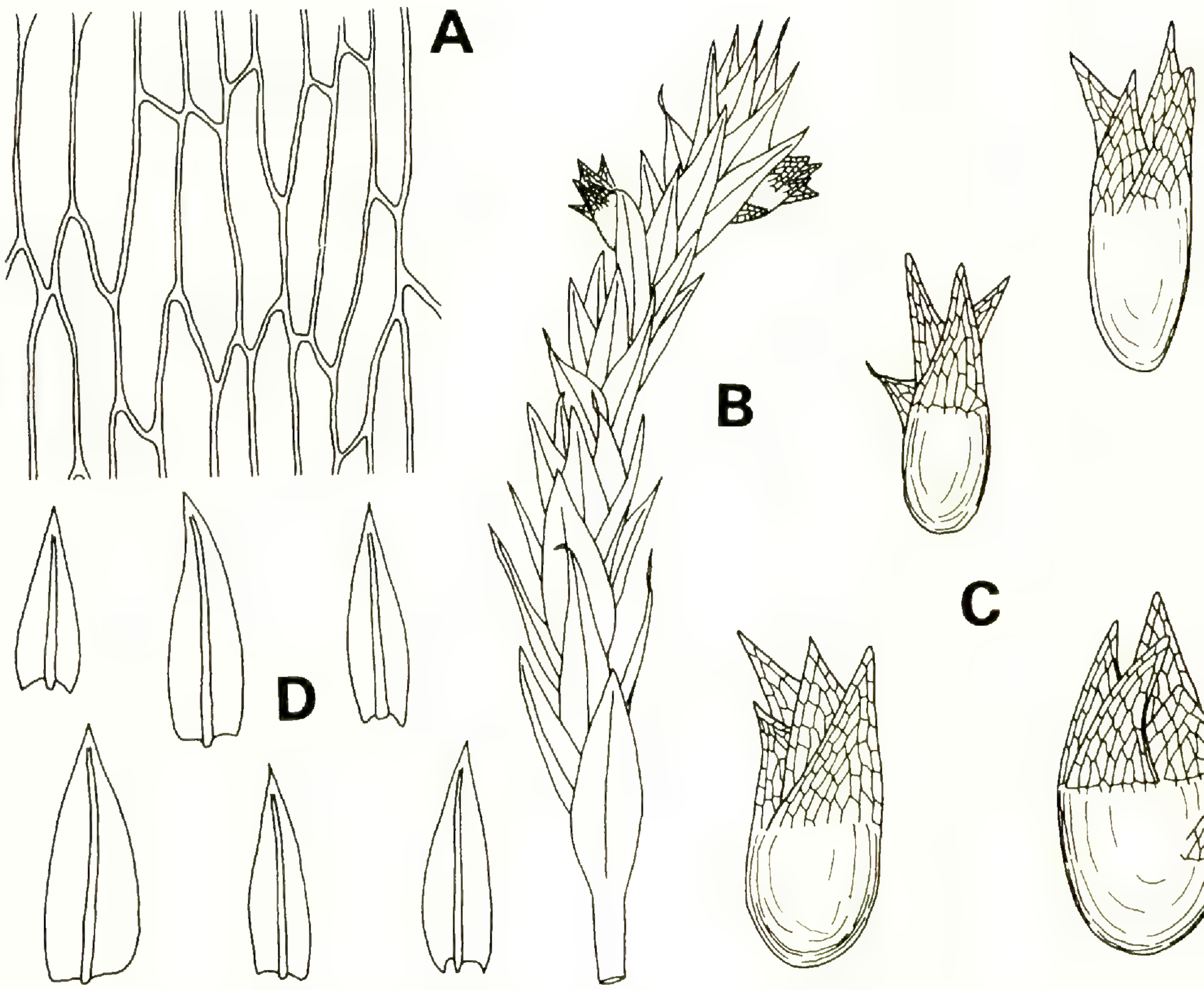


FIG. 21. *Pohlia beringiensis*. A. Upper leaf cells, ×290. B. Habit, ×10. C. Gemmae, ×100. D. Leaves, ×22.

Pohlia beringiensis was mentioned previously (Shaw 1981, p. 33) as a variant possibly related to *P. drummondii*. Continued study has convinced me that it should be segregated as a new species. Compared to *P. drummondii*, plants of *P. beringiensis* are very small, with leaves whitish, erect and slenderly lanceolate. The gemmae are of a similar form to those of *P. drummondii*, but are even more deeply cherry red (at least when fresh). Red gemmae on plants with such pale, whitish leaves gives *P. beringiensis* an aspect different from any expression of *P. drummondii*.

The micro-habitat in which *P. beringiensis* occurs also differs from that of *P. drummondii*. In western North America, *P. drummondii* grows on relatively organic-rich soil banks or frequently in alpine tundra (Shaw 1982), whereas *P. beringiensis* prefers sandy or muddy, organic-poor sites such as roadside drainage ditches. Even allowing for some variation in the microhabitats occupied by *P. drummondii*, there does seem to be ecological differences between the two.

Especially since sporophytes of *P. beringiensis* are not known, differences between it and *P. drummondii* are mainly with respect to aspect, color, size and habitat of plants. The gemmae, in terms of size and development, are similar to those of *P. drummondii*, differing only in color. Varietal status for *P. beringiensis* (under *P. drummondii*) could be defended, and there is no correct answer to the problem of appropriate rank. Other pairs of *Pohlia* species are distinguished by such ill-defined features as habit and color. For example, few collectors confuse *P. melanodon* and *P. wahlenbergii*, although they differ only in size and sheen. The distribution of *P. beringiensis*, seemingly disjunct from central Asia (Altai Mts.) to Alaska and the Yukon Territory, falls more or less within the circumboreal range of *P. drummondii*. In northwestern North America, *P. drummondii* is far

more common than *P. beringiensis*. In addition to my own collections of *P. beringiensis* (seven) it has otherwise been collected only twice: Alaska, Liberator Lake, Steere *610723–39* (NY), and U.S.S.R. (or China), Altai Mts., *Barzduna*, 1966 (NICH).

POHLIA ANNOTINA AND RELATED SPECIES

Species of this group, characterized by axillary gemmae, were revised by Shaw (1981a). Brief descriptions, and illustrations of gemmae are provided here but the reader is referred to Shaw (1981a & b) for a more detailed treatment.

All nine species are virtually uniform sporophytically, characterized especially by rectangular, sinuose exothecial cells and well-developed peristomes with endostome segments hyaline, broadly keeled and perforate.

18. **Pohlia drummondii** (C. Müll.) Andr. *in* Grout, Moss Fl. N. Am. 2. 196. 1935.

Medium-sized, glossy plants with red stems (when fresh). Gemmae arising singly in 1–3(–5) upper leaf axils (sometimes lacking in alpine plants), oblong-bulbiform, 350–600 μm long, green when young, red when older, with 3–6 lanceolate-laminate leaf primordia scattered at the apex and below, the primordia generally green. Fig. 22A.

Roadbanks, streambanks and gullies in montane areas, frequent on non calcareous tundra soil. Circumboreal, in North America south to California, Colorado and New England. Map 19.

19. **Pohlia filum** (Schimp.) Mårt., Svensk Vet.–Ak. Arh. Natur. 14: 149. 1956.

Slender, rather glossy plants frequently black below when dry. Leaves erect, imbricate to remote. Gemmae arising singly in 1–3(–5) upper leaf axils, egg-shaped, 300–600 μm long, green when young, orange to orange-brown when older, frequently becoming black when dry, with 3–6 rather stiff, triangular-lanceolate leaf primordia at the apex and sometimes lower, the primordia green to pale. Fig. 22B.

Common on glacial outwash in northwestern North America, rarely along roadsides, restricted to nearly organic-free soils. Circumboreal; in North America south to Oregon, Alberta, Quebec and Prince Edward Island. Map 20.

Pohlia filum is distinguished from *P. drummondii* by its slender habit, erect leaves, and egg-shaped gemmae with stiffly appearing primordia often restricted to the gemmae apex.

20. **Pohlia andalusica** (Höhn.) Broth. *in* Engler and Prantl, Nat. Pfl. 1(3): 551. 1903.

Slender, glossy plants with erect, ± imbricate leaves. Gemmae in clusters of 3–8 in 1–4 upper leaf axils, obconic to oblong, 250–500 μm long, green when young, brown to red-brown when older, with 3–6 lanceolate-laminate leaf primordia more or less restricted to the apex, the primordia green. Fig. 22C.

On soil in disturbed sites; rare in western North America, from Alaska and the Yukon south to Washington and Colorado; more frequent in northern New York, New England and the Maritime provinces. Map 21.

Pohlia andalusica is distinguished from related species by its slender, glossy appearance and gemmae with laminate primordia arising in clusters in a few upper leaf axils.

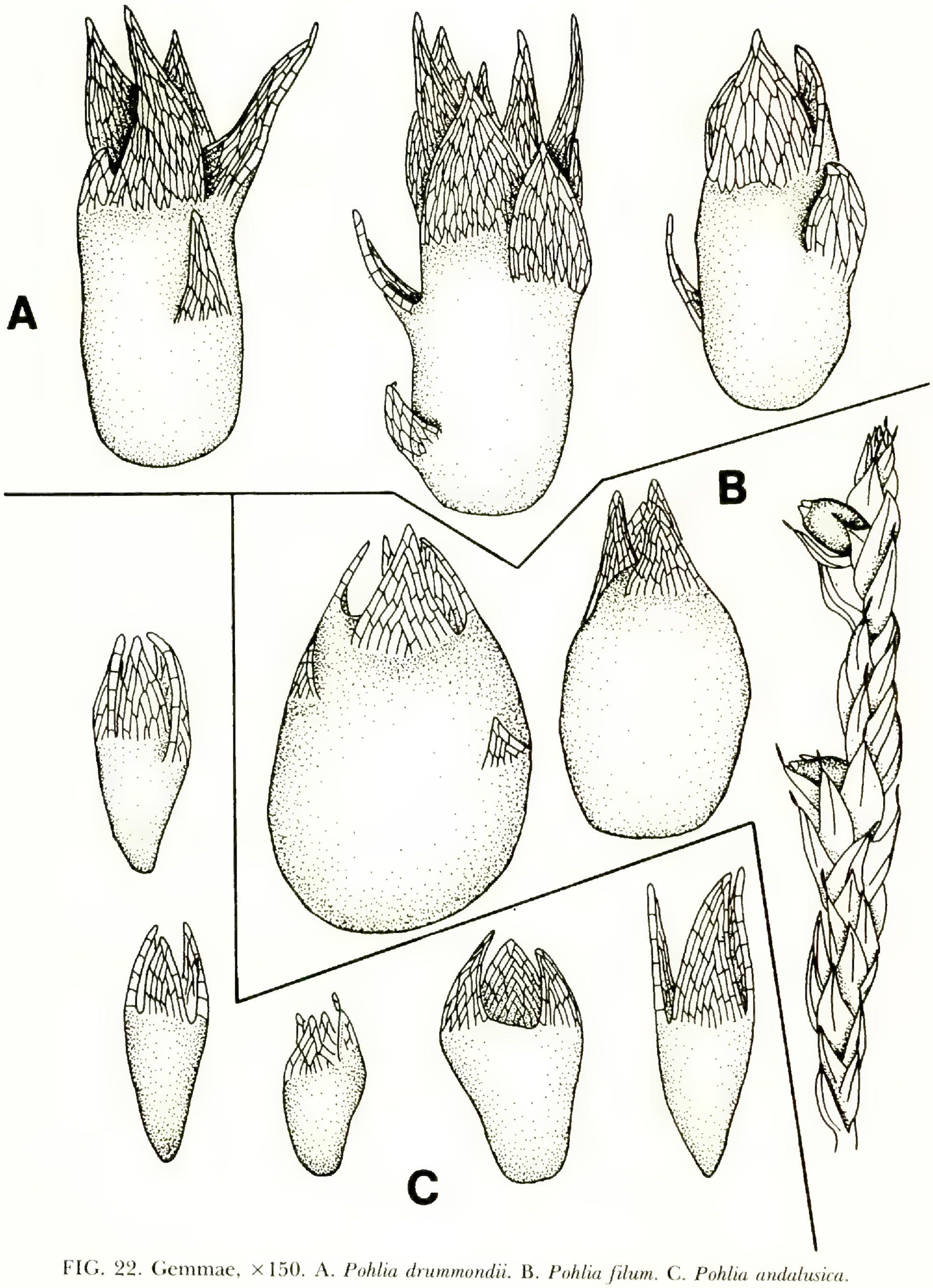


FIG. 22. Gemmae, ×150. A. *Pohlia drummondii*. B. *Pohlia filum*. C. *Pohlia andalusica*.

21. **Pohlia tundrae** Shaw, The Bryologist 84: 65. 1981.

Medium-sized, glossy plants commonly forming compact turfs on tundra soil, more lax and elongate in protected sites. Gemmae in clusters of 3-many in the upper leaf axils, cylindrical to linear-oblong, 275–500 μm long, hyaline, green or red-brown, with 3–6 flexuose, lanceolate-laminate leaf primordia at the apex and frequently lower on the body, the primordia green. Fig. 23A.

Common on alpine and subalpine soil, less frequent along roadbanks and in other disturbed sites below treeline. Endemic to western North America; Wash-

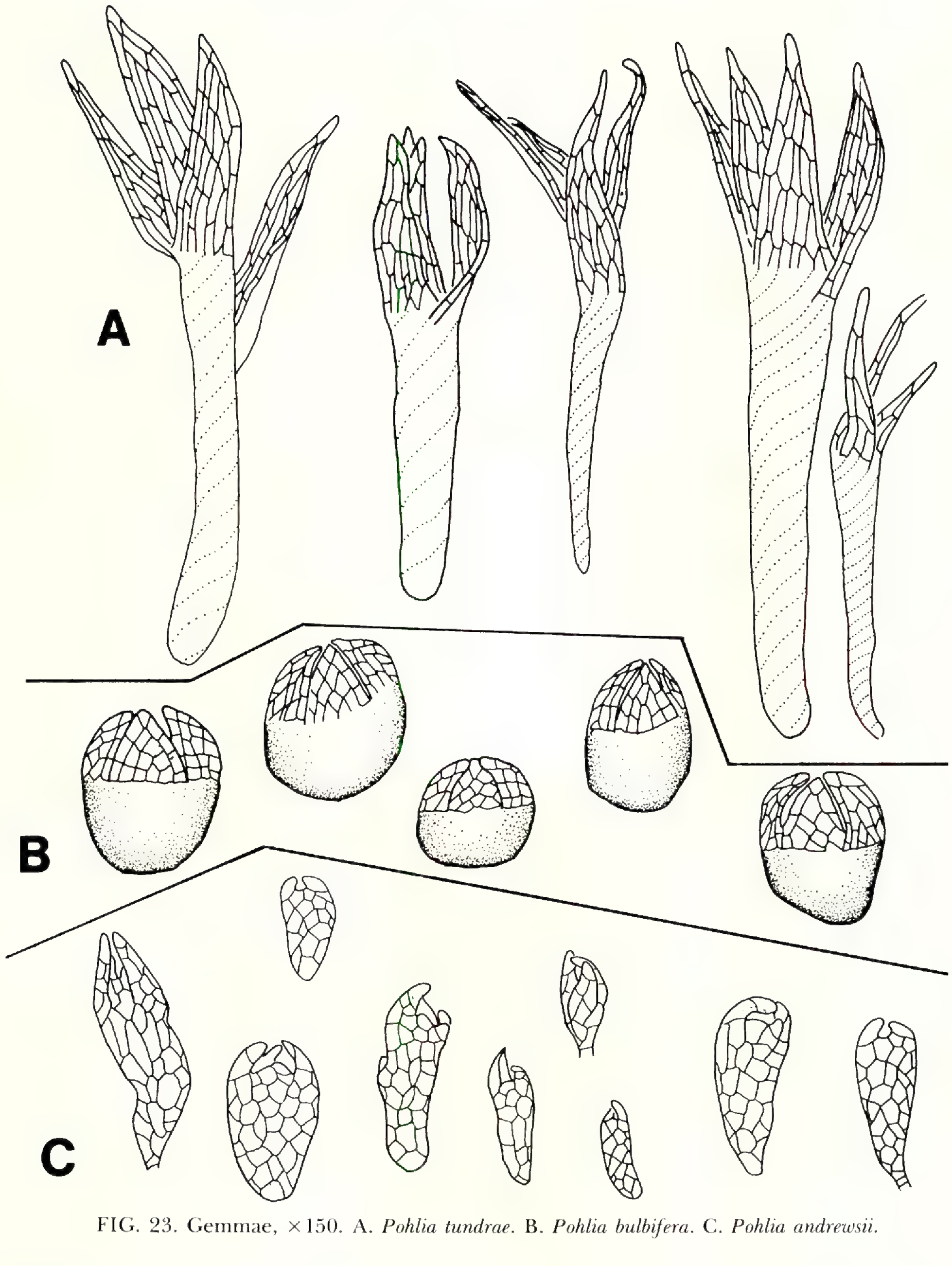


FIG. 23. Gemmae, ×150. A. *Pohlia tundrae*. B. *Pohlia bulbifera*. C. *Pohlia andrewsii*.

ington and Montana south to California and Arizona; northern British Columbia and southern Alaska. Map 21.

The narrowly cylindrical gemmae distinguish *P. tundrae* from other species with laminate leaf primordia. It differs from *P. annotina* in having glossy leaves in addition to the gemmae characters given in the key.

22. **Pohlia bulbifera** (Warnst.) Warnst., Krypt. Fl. Brandenburg 2: 429. 1904.

Slender, glossy plants forming compact turfs. Leaves wide-spreading. Gemmae in clusters of 3–8 in upper leaf axils, spherical to obovate, 200–400 μm in the longest dimension, green to yellow, yellow-orange, or orange-red, with 4–5 broadly triangular-laminate leaf primordia in a tight spiral (almost whorled)

at the apex, the primordia green, incurved over the apex and forming a dome. Fig. 23B.

On soil in disturbed places, often where the ground is compacted and hard. Circumboreal; rare in western North America (Alaska, Yukon Territory, Alberta and Colorado), more common in northern New York, New England, and the Maritimes, west to Michigan and Wisconsin. Map 23.

Pohlia bulbifera is known at once by glossy leaves and more or less spheroidal gemmae with the laminate leaf primordia forming a dome over the apex.

23. **Pohlia andrewsii** Shaw, The Bryologist 84: 70. 1981.

Medium size to robust shiny plants forming small populations in rock crevices. Gemmae in clusters of 4-many in the upper leaf axils, oblong to linear-oblong or spheroidal, 50–170 μm long, pale green when young, red to orange-red when older, strongly translucent, with 1–4(–6) short, incurved, peglike leaf primordia at the apex or rarely lower, the primordia of some gemmae becoming laminate with age. Fig. 23C.

Soil in rock crevices in tundra habitats, less commonly along roadbanks. Arctic and subarctic North America, Greenland, Spitzbergen, Norway, Sweden and Czechoslovakia. Map 22.

Pohlia andrewsii may be recognized by glossy leaves and orange to red, translucent gemmae with the primordia, whether peglike or laminate, incurved over the apex.

24. **Pohlia proligera** (Lindb. *ex* Breidl.) Lindb. *ex* Arn., Bot. Not. 1894: 54. 1894.

Medium-sized to robust, glossy plants forming small to extensive populations. Gemmae in dense clusters in upper leaf axils, linear-vermicular to narrowly oblong, 65–110 μm long, green when young, yellow to golden, orange, pink or sometimes red when older, strongly translucent, with 1–2 peglike apical leaf primordia, the primordia (when single) often bent at an angle to the propagulum body. Fig. 24A.

On soil, especially along the sides of roads, paths and streams; sometimes on disturbed tundra soil in the far North but rarely reaching the alpine zone in more southerly mountains; rarely on rotting wood. Circumboreal; our most common propaguliferous species across northern North America, south to California, Colorado, Wisconsin, Michigan and southern New England. Map 25.

Pohlia proligera is well characterized by glossy leaves and linear-vermicular gemmae forming a felty mass in upper leaf axils. The gemmae are uniform in shape and have only one or two apical primordia.

The type specimens of *P. proligera* are located in GJO–Breidler rather than GZU as previously stated (Shaw 1981b, p. 21).

25. **Pohlia annotina** (Hedw.) Lindb., Musci Scand. 17. 1879.

Dull, slender plants often forming ± extensive turfs. Gemmae in clusters of 5-many in the upper leaf axils, extremely variable in shape, oblong, obconic or ± elongate and linear, although almost always tapered to the base, rarely oblong-bulbiform when old, 150–300 μm long, occasionally longer, hyaline, yellow, green, orange or red when young, generally orange-red when large and bulbiform, strongly translucent, with (2–)3–5 peglike, erect, apical leaf primordia, the primordia occasionally becoming 2–4 cells broad at the base on old gemmae. Fig. 24B.

Common in disturbed habitats; sandy soil in gardens, on roadbanks and in gullies, rarely found in undisturbed sites. Possibly circumtemperate; specimens

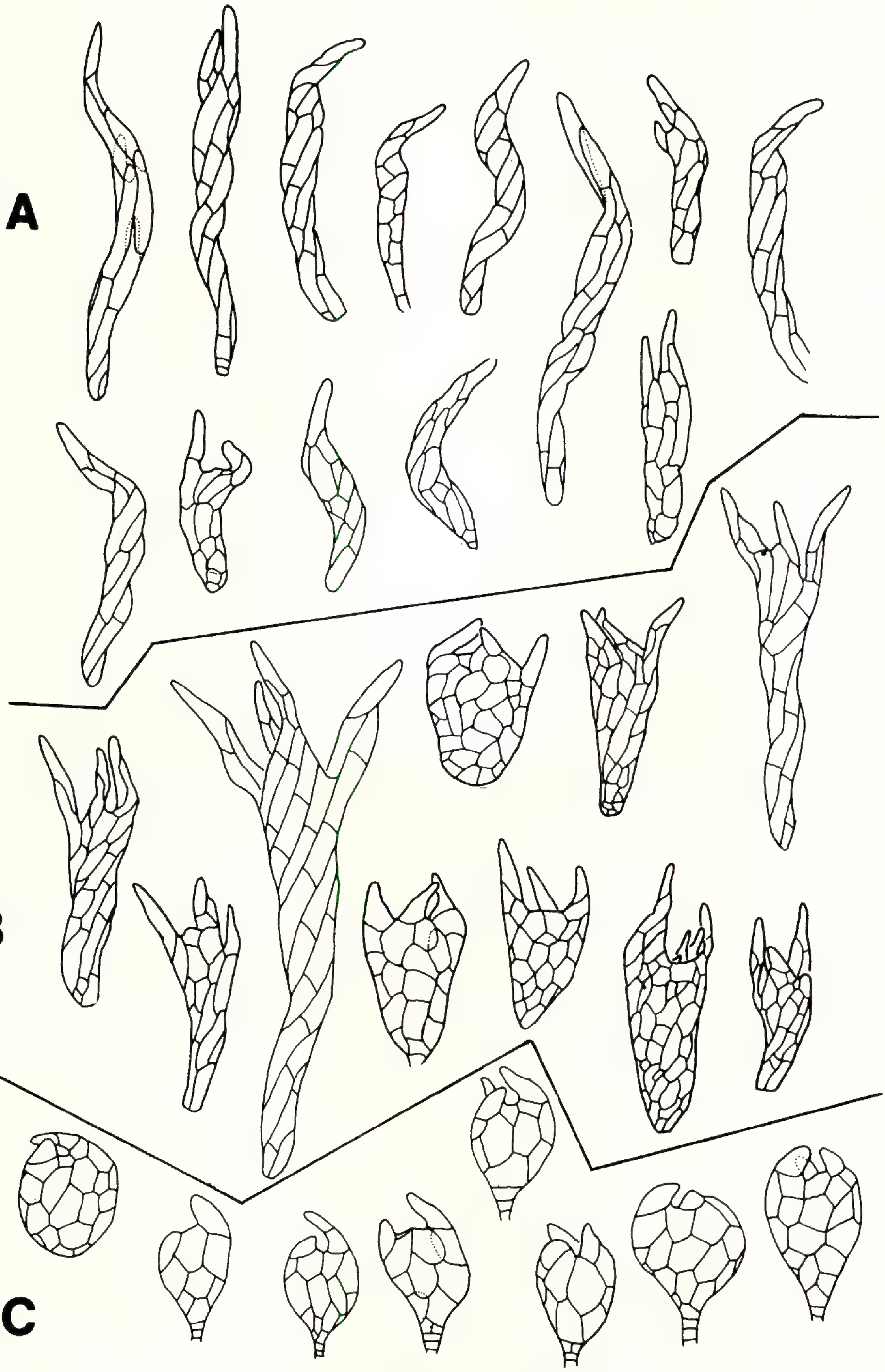


FIG. 24. Gemmae, ×150. A. *Pohlia proligera*. B. *Pohlia annotina*. C. *Pohlia camptotrachela*.

confirmed from northern and central Europe and North America. Bicentric in North America and having a suboceanic distribution: Newfoundland to Georgia and Arkansas, Wisconsin, Missouri and Iowa; Alaska, British Columbia, Montana, Washington, Oregon and California. Map 26.

Characterized by dull leaves and oblong to linear-obconic gemmae with

peglike leaf primordia, *P. annotina* can be confused only with *P. camptotrachela*. From *P. proligera* it is distinguished by dull leaves and gemmae having three to as many as five primordia.

26. **Pohlia camptotrachela** (Ren. & Card.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Slender, dull plants forming small isolated populations. Gemmae in clusters of 5-many in upper leaf axils, uniform in shape, spheroidal or slightly longer than wide, 70–120(–150) μm in the longest dimension, yellow or occasionally brown, strongly translucent, with 1–4 short, peglike leaf primordia at the apex, the primordia incurved over the apex or less commonly erect. Fig. 24C.

Not uncommon on soil of roadbanks, pathbanks and stream margins in montane areas along the Sierra Nevada–Cascade systems; rather poor alpine soil in the central Rockies. Western North America (British Columbia south to California, Nevada and Colorado); the British Isles, central and northern Europe. Map 27.

Unlike *P. annotina*, the gemmae of *P. camptotrachela* are uniform in shape and size: roughly spheroidal and less than 150 μm in diameter. Among the North American propaguliferous species, only *P. annotina* and *P. camptotrachela* have notably dull leaves. Virtually identical male plants of the two species give further indication of a close relationship.

27. **Pohlia pacifica** Shaw, sp. nov.

Plantae erectae, graciles, valde nigrescentes. Caulis simplex, e basi innovans et ramulosus, erectus, 1.0–8.0 mm altus. Folia inferiora lanceolata, comalia elongato-lanceolata, ad apicem valde serrata, cellulis linearibus, angustis. Peristomia duplices, exostomii dentibus 16, luteo-bruneis. Annulus latus, duplex vel triplex.

Slender, pale green, shiny plants usually in small populations. Stems 2–8 mm, simple when sterile or bearing gametangia. Leaves erect-spreading to spreading when moist, scarcely altered on drying, 1.1–1.8(–2) mm long, 0.5–0.8 mm wide, lanceolate, acute to shortly acuminate, not or slightly keeled, not to slightly decurrent; margins plane, coarsely serrate near the apex, entire to subentire below; costa ending 3–5 cells below the apex; upper cells linear-rhomboidal, vermicular, thin-walled, (100–)115–135(–150) μm long, 6–9 μm wide, somewhat longer and narrower along the margin (to ca. 180–200 μm). Dioicous; perigonia bulbiform; outer bracts ± longly acuminate, spreading to erect-spreading from an erect base, serrate near the apex; perichaetia rather conspicuous, outer bracts to 3.2 mm long, narrowly and longly lanceolate. Sporophytes frequent in spring; setae 5–10 mm long; capsules inclined 120°–180° from vertical, 1.5–2.5 mm long, orange to tan, pyriform, the neck shorter and narrower than the urn; exothecial cells shortly rectangular, 25–55 μm long, 12–25 μm wide, with evenly thickened, strongly sinuose walls; stomata superficial, 35–55 μm long; annuli of 2(3) rows of cells, separating irregularly; opercula convex-conic, obtuse or rarely acute; exostome teeth yellow-brown, narrowly acute, bordered, trabeculate, coarsely papillose near the apex dorsally, more finely roughened below; endostome hyaline; segments keeled and broadly perforate; basal membrane about ½ the height of the exostome teeth; cilia short to long, usually nodulose. Spores 14–20 μm, nearly smooth. Fig. 25.

TYPE: U.S.A. California, Del Norte Co.: Del Norte Redwoods State Park, southern boundary, clay roadbank, 15 April 1980, *Shaw 4173* (Holotype: MICH; Isotype: J. Shaw). Paratypes: Oregon, Tillamook Co.: 2.7 mi N of Arcada Beach on Hwy. 101, muddy roadbanks and drainage ditches, 14 April 1980, *Shaw 4110*

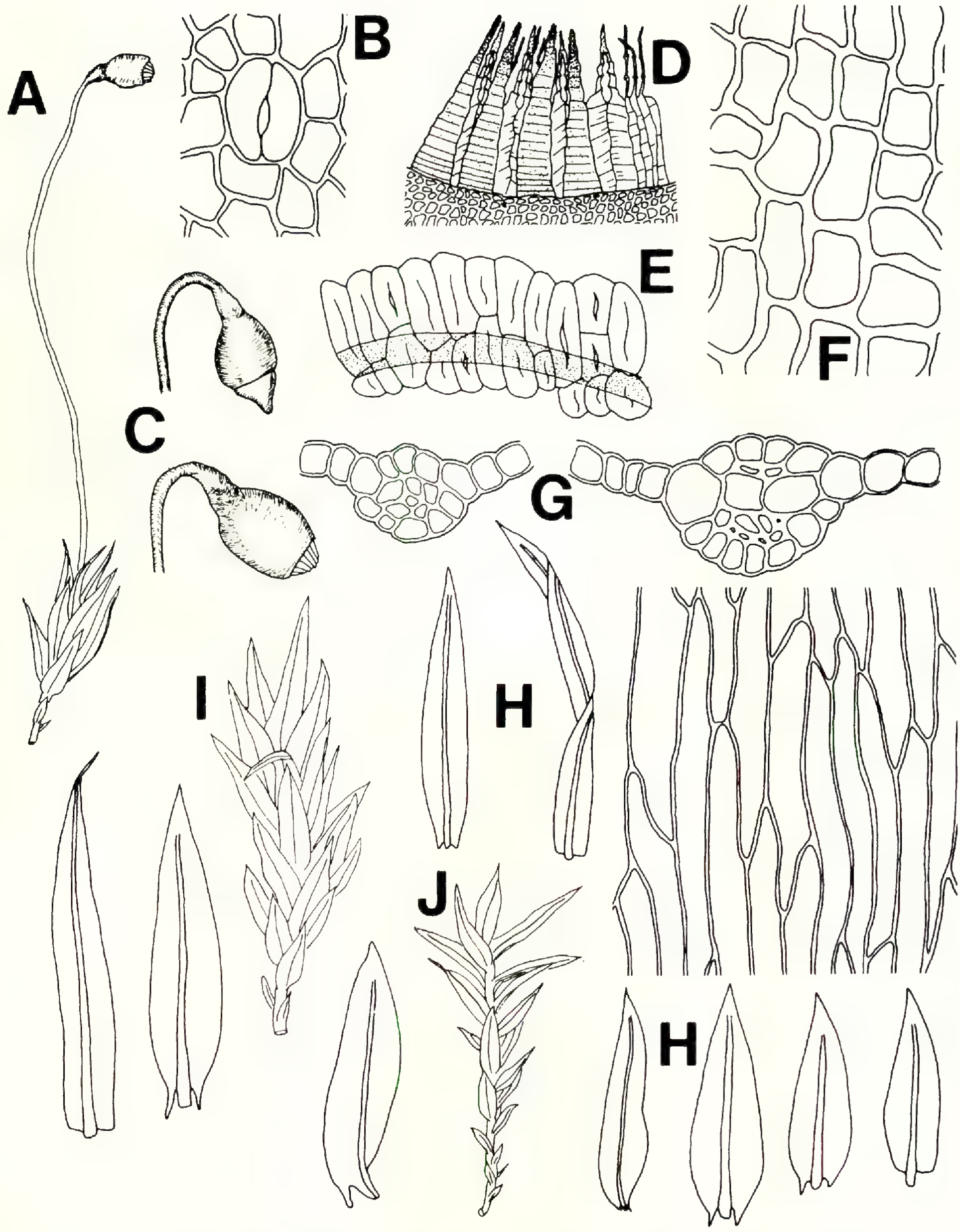


FIG. 25. *Pohlia pacifica*. A. Habit, ×3. B. Stomate, ×230. C. Capsules, ×12. D. Peristome, ×64. E. Annulus, ×232. F. Exothecial cells, ×232. G. Costae, transverse sections near the apex (left) and base (right), ×232. H. Leaves, ×17. I. Habit, female plant, ×3. J. Habit, sterile plant ×3. K. Upper leaf cells, ×232.

(CANM), 4127 (NY). Washington, Clallam Co.: Sol Duc Hot Springs, *Lawton 4298* (WTU).

Acidic, sandy or clay soil, especially in wet, disturbed places at sea level; drainage ditches, stream banks. Endemic to the Pacific Coast of North America; Queen Charotte Islands of British Columbia (*Schofield 14172a*, UBC), Washington, Oregon, California (south to Santa Cruz County). Map 28.

Pohlia pacifica generally grows in the same habitats with *Epipterygium tozeri* (Grev.) Lindb. and *P. longibracteata*. It is frequently mixed with the *Epipterygium*,

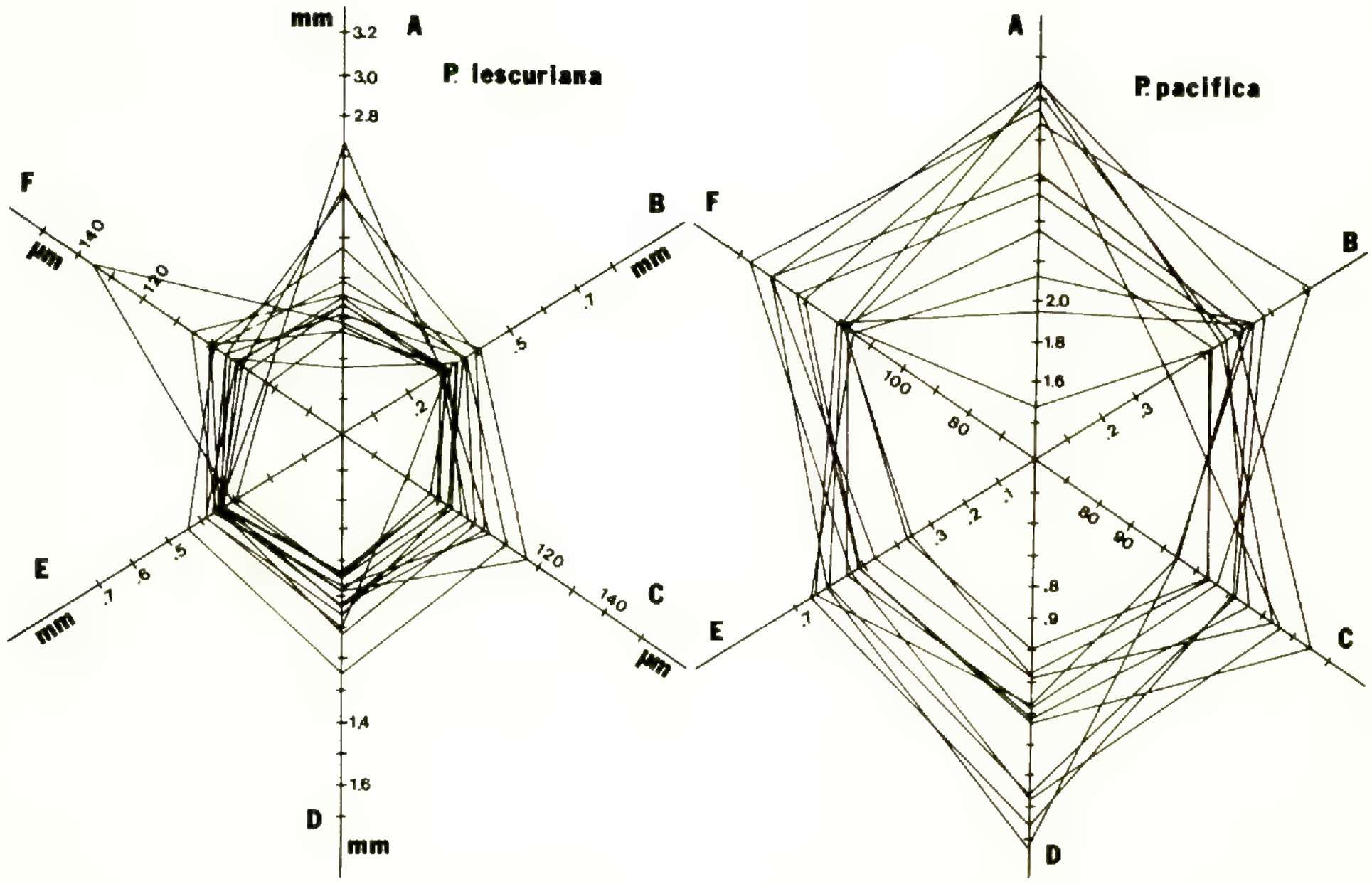


FIG. 26. Polygraph comparing poulations of *Pohlia lescuriana* and *Pohlia pacifica*. A. Perichaetial leaf length. B. Perichaetial leaf width. C. Branch leaf cell length. D. Branch leaf length. E. Branch leaf width. F. Perichaetial leaf cell length. Lines connect values for different measurements from one specimen.

whereas *P. longibracteata* prefers wetter sites (sometimes a few feet away) that are periodically submerged. *Pohlia longibracteata* is much larger (8–15 mm), lacks an annulus and has immersed stomates. *Epipterygium tozeri* is the same size as *P. pacifica* but has dull, bluish leaves, with broad cells (14–25 μm wide), and strongly collenchymatous exothecial cells.

Pohlia pacifica is closely related to *P. lescuriana* but is distinguished by the more robust habit, very glossy leaves and longer cells. Figure 26 compares populations of the two species with respect to six morphological characters; *P. pacifica* is more robust in all respects. Although many populations of *P. lescuriana* have rhizoidal gemmae, I have seen one or two apparently attached to *P. pacifica* only once, as pointed out to me by A. C. Crundwell in a specimen sent for his opinion.

Tan, Shaw and Ireland (1981) reported *P. lescuriana* from western North America, but several of the specimens have proved to be misidentified. I can confirm *P. lescuriana* in the west on the basis of only two collections from Alaska: Curry, *Schofield 1892* (BH); Kenai Peninsula, *Shaw 4016* (MICH).

28. **Pohlia lescuriana** (Sull.) Grout, Moss. Handlens Microsp. 210. 1906.
Bryum pulchellum Hedw., Spec. Musc. 180. 1801.
Hypnum pulchellum (Hedw.) Web. & Mohr, Ind. Musc. Crypt. 3. 1803.
Bryum carneum var. *pulchellum* (Hedw.) Turn., Musc. Hib. 119. 1804.
Mnium pulchellum (Hedw.) P. Beauv., Prodr. 76. 1805.
Bryum tenellum Brid., Bryol. Univ. 1: 653. 1826 (*nom. nud. in synon.—B. pulchellum*).
Webera pulchella (Hedw.) Fuernr., Flora 12(Ergbl. 2): 35. 1829.
W. carnea var. *pulchella* (Hedw.) Hampe, Flora 20: 277. 1837.
Bryum lescurianum Sull., Mem. Am. Ac. Arts. Sci. n. ser. 4: 171. 1849.
Webera lescuriana (Sull.) Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 1875.
Pohlia pulchella (Hedw.) Lindb., Musci Scand. 17. 1879.

Webera iwozanica Besch., Ann. Sci. Nat. Bot. ser. 7. 17: 342. 1893.
Mniobryum pulchellum (Hedw.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

Tiny, dull or somewhat glossy plants. Stems 2–8 mm, simple when sterile or bearing gametangia. Leaves erect-spreading on sterile plants, few, erect, and overlapping on fertile plants, 0.8–1.4 mm long, serrulate near the apices; upper cells linear-rhomboidal, 65–110 μm long, 6–9 μm wide, with thin walls. Tubers sometimes present on rhizoids, orange, orange-brown or yellow, 70–120 μm long. Dioicous; perichaetial bracts linear-lanceolate to lanceolate, to 2.5 mm long; perigonial bracts ± longly acuminate, erect to erect-spreading. Capsules inclined 95°–180° from vertical, shortly and broadly pyriform, 1.5–3.0 mm long; exothecial cells short-rectangular, 12–40 μm long, with strongly sinuose walls; stomates superficial or slightly sunken; annuli of 1–3 cell rows, separating irregularly; opercula low to high conic; exostome teeth light yellow-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose, rarely short. Spores 18–26 μm, distinctly roughened. Fig. 27.

Uncommon; on soil, often in weedy places, roadbanks, fields, stream banks, near sea level. Fennoscandia; British Isles; Central Europe; Japan; North America; Maritime provinces and New England south to Virginia and Tennessee, west to Michigan and Iowa; disjunct in Alaska, where it is known from the Kenai Peninsula and near Curry on the southern edge of the Alaska Range. Map 28.

Exsiccati: Austin, Musci Appal. 190 as *B. lescurianum* (CANM, CAS, MICH, UBC); Brotherus, Bryoth. Fenn. 45 as *P. pulchella* (BH); Grout, N. Am. Musci Perf. as *P. lescuriana* (CANM, CAS, COLO, MICH, NY, UBC, UC); Hartman, Bryac. Scand. Exs. 404 as *W. pulchella* (BH); Holzinger, Musci Acro. Bor.–Amer. 220 as *W. lescuriana* (CANM, MICH, UC; =*P. wahlenbergii* in COLO); Husnot, Musci Gall. 572 as *W. pulchella* (BH); Macoun, Canad. Musci 163 as *W. lescuriana* (CANM: =*P. annotina* in UC); Renauld and Cardot, Musci Am. Sept. Exs. 222 as *W. lescuriana* (BH, CANM); Sull., Musci Allegh. 101 as *B. pulchellum* (MICH); Sull. & Lesq., Musci Bor. Am. (ed. 1) 181 as *B. lescurianum* (BH, MICH); (ed. 2) 273 as *B. lescurianum* (BH, CANM, MICH).

One of the tiniest species, *P. lescuriana* looks much like a miniature *P. annotina* without gemmae. It is characterized by the slight stature, well-developed peristome, sinuose exothecial cells, separating annuli and superficial (or slightly sunken) stomates. I find that North American plants sometimes, but not always, have gemmae on their rhizoids. These range from scarce to abundant and are orange to yellow, round to ovoid, 70–120 μm in diameter, and without bulging superficial cells.

The European *P. lutescens* (Limpr.) H. Lindb. is distinguished from *P. lescuriana* by its stellate rhizoidal gemmae (Whitehouse 1973, 1978), although very similar in most other respects. Ecological and phytogeographic information needs to be accumulated with which to evaluate *P. lutescens* as a biological entity.

29. **Pohlia wahlenbergii** (Web. & Mohr) Andr. *in* Grout, Moss Fl. N. Am. 2: 203. 1935.
Hypnum albicans [Wahlenb. *ex*] Web. & Mohr, Ind. Musc. Pl. Crypt. 3. 1803. (*nom. nud.*).
Hypnum wahlenbergii Web. & Mohr, Bot. Taschenb. 280, 475. 1807 (type not seen).
Mnium albicans Wahlenb., Fl. Lapp. 353. 1812 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).
Bryum wahlenbergii (Web. & Mohr) Schwaegr., Spec. Musc. Suppl., 1(2): 92. 70. 1916.

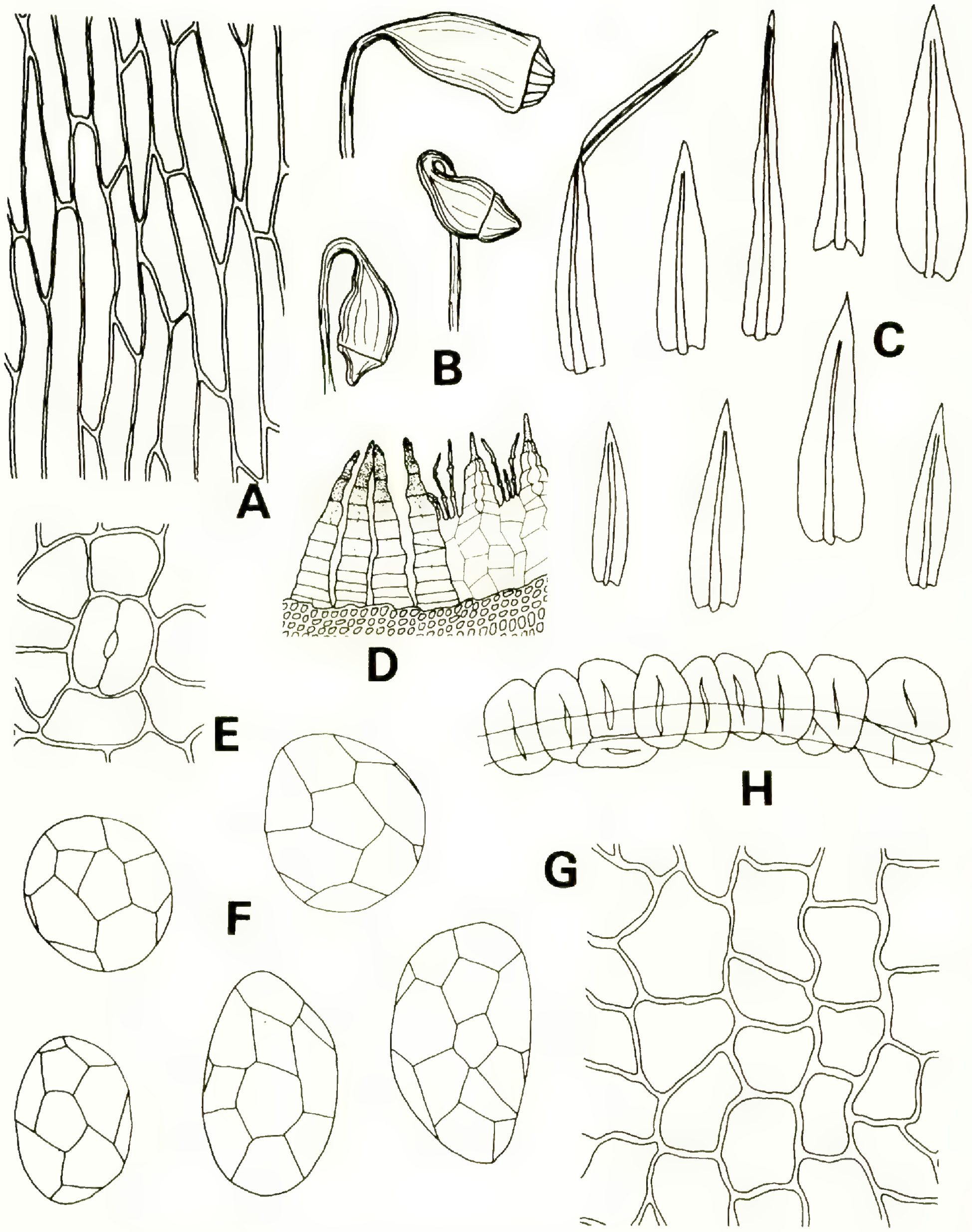


FIG. 27. *Pohlia lescuriana*. A. Upper leaf cells, ×290. B. Capsules, ×15. C. Leaves, ×22. D. Peristome, ×80. E. Stomate, ×290. F. Rhizoidal tubers, ×270. G. Exothecial cells, ×290. H. Annulus, ×290.

B. nitens Sw. *ex* Schwaegr., Spec. Musc. Suppl., 1(2): 92. 1816 (*nom. nud. in synon.—B. wahlenbergii*).

B. glaciale Brid., Bryol. Univ. 1: 852. 1826. (Lectotype: B–Brid.).

Webera wahlenbergii (Web. & Mohr) Fuernr., Flora 12(Ergbl. 2): 35. 1829.

Bryum wahlenbergii var. *glaciale* (Brid.) Hueb., Musc. Germ. 456. 1833.

Webera wahlenbergii var. *glacialis* (Brid.) Hampe, Flora 20: 277. 1837.

Webera albicans Schimp., Coroll. 67. 1856 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

W. albicans var. *glacialis* (Brid.) Schimp., Coroll. 67. 1856.

Lamprophyllum albicans Lindb., Oefv. K. Vet. Ak. Foerh. 23: 75. 1886 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

Pohlia albicans Lindb., Musci Scand. 17. 1879 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

P. albicans var. *glacialis* (Brid.) Broth. & Sael., Act. Soc. F. Fl. Fenn. 6(4): 59. 1890.

Mniobryum albicans Limpr., Laubm. Deutschl. 2: 277. 1892 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

Pohlia obtusata Kindb., Rev. Bryol. 32: 37. 1905. (Lectotype: S–Kindb.).

Mniobryum wahlenbergii (Web. & Mohr) Jenn., Man. Moss. W. Penn. 146. 18. 1913.

Mniobryum wahlenbergii var. *glaciale* (Brid.) Wijk & Marg., Taxon 8: 74. 1959.

Very robust to slender, dull, whitish plants forming small populations or covering large areas. Stems 4–15(–50) mm, simple when slender and sterile, forking when robust and fertile, with 1–3 innovations below perichaetia or perigonia; leaves erect-spreading, crowded to remote, 0.9–1.8 mm long, toothed to serrulate in the upper ⅓, acute or sometimes ± rounded at the apex, ± longly decurrent; upper cells broadly oblong-hexagonal, 65–110 μm long, 12–20(–30) μm wide, gradually longer and narrower near the margin, with thin to firm walls. Dioicous; perichaetial bracts scarcely differentiated, to 2.0 mm long; perigonial bracts shortly acuminate, wide-spreading. Capsules inclined 140°–240° from vertical, shortly and broadly pyriform or urceolate, 1.5–2.5 mm long; exothecial cells ± isodiametric, 22–55 μm, with strongly sinuose walls; stomates ± deeply immersed; annuli lacking; opercula low-convex to conic, apiculate; exostome teeth light brown to red-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline to yellow; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 13–18(–24) μm, very finely roughened. Fig. 28.

On calcareous rocks or soil in wet seepy areas, ditches, stream margins, springs, glacial outwash; sea level to the alpine zone. Widespread in North America (across Canada and south to California, Arizona, Arkansas and North Carolina), Europe, and northern Asia; Iceland; Greenland; Mexico (Baja California, Distrito Federal, Michoacán, Oaxaca, Puebla, Sonora); Guatemala (Quezaltenango, San Marcos); Dominican Republic (*Shaw 5656*); Chile; Argentina; Australia (also reported from New Zealand); Japan. Map 29.

Exsiccati: Allen, Moss. Cascade Mts. 53 as *P. albicans* (DUKE, MICH, NFLD); Bauer, Musci Eur. Exs. 915 as *M. albicans* (WTU); Drummond, Musci Amer. 260 as *B. carneum* (CANM, MICH, NY); Grout, N. Am. Musci Perf. 260 as *M. carneum* (UC); Holmen, Bryoph. Dan. Exs. 151 as *W. albicans* (ALTA, NFLD, UC); Holzinger, Musci Acro. Bor.–Am. 168 as *M. albicans* (MICH, UC); 220 as *W. lescuriana* (COLO); 393 as *M. albicans* (MICH, UC); 437 as *M. albicans* (MICH, UC, WTU); Kobsch, Bryoth. Sax. 52 as *M. albicans* (MICH); 244 as *M. albicans* (MICH); 420 as *P. commutata* (MICH); Macoun, Canad. Musci 165 as *W. albicans* (MICH); 208 as *W. carnea* (CANM); Migula, Krypt. Germ., Aust., Helv. Exs. 228 as *M. albicans* (MICH); Rabenhorst, Bryoth. Eur. 1215 as *W. ludwigii* (MICH); Ren. & Card., Musci Am. Sept. Exs. 303 as *W. albicans* (MICH); Savicz-Ljubitzkaja, Hep. Musci URSS Exs. 126 as *M. wahlenbergii* (WTU); 127 as *M. wahlenbergii* v. *glaciale* (WTU); Schofield, Bryoph. Can. 9 as *P. wahlenbergii* (ALTA, CANM, NFLD); Sull. & Lesq. Musci Bor.–Am. (ed. 1) 100 as *B. wahlenbergii* (MICH); 182 as *B. wahlenbergii* (MICH); ed. 2, 274 as *B. wahlenbergii* (MICH); Warnst. Märk. Laubm. 172 as *W. albicans* (CAS).

Distinguished by rather dull, whitish-green leaves, *P. wahlenbergii* is one of the most common Pohlias of the northern United States and Canada. It is most luxuriant in seepy calcareous areas at high altitudes and latitudes, where the stems may attain a height of several centimeters and the leaves are darker green on deep red stems. In ecologically or geographically marginal sites, *P. wahlen-*

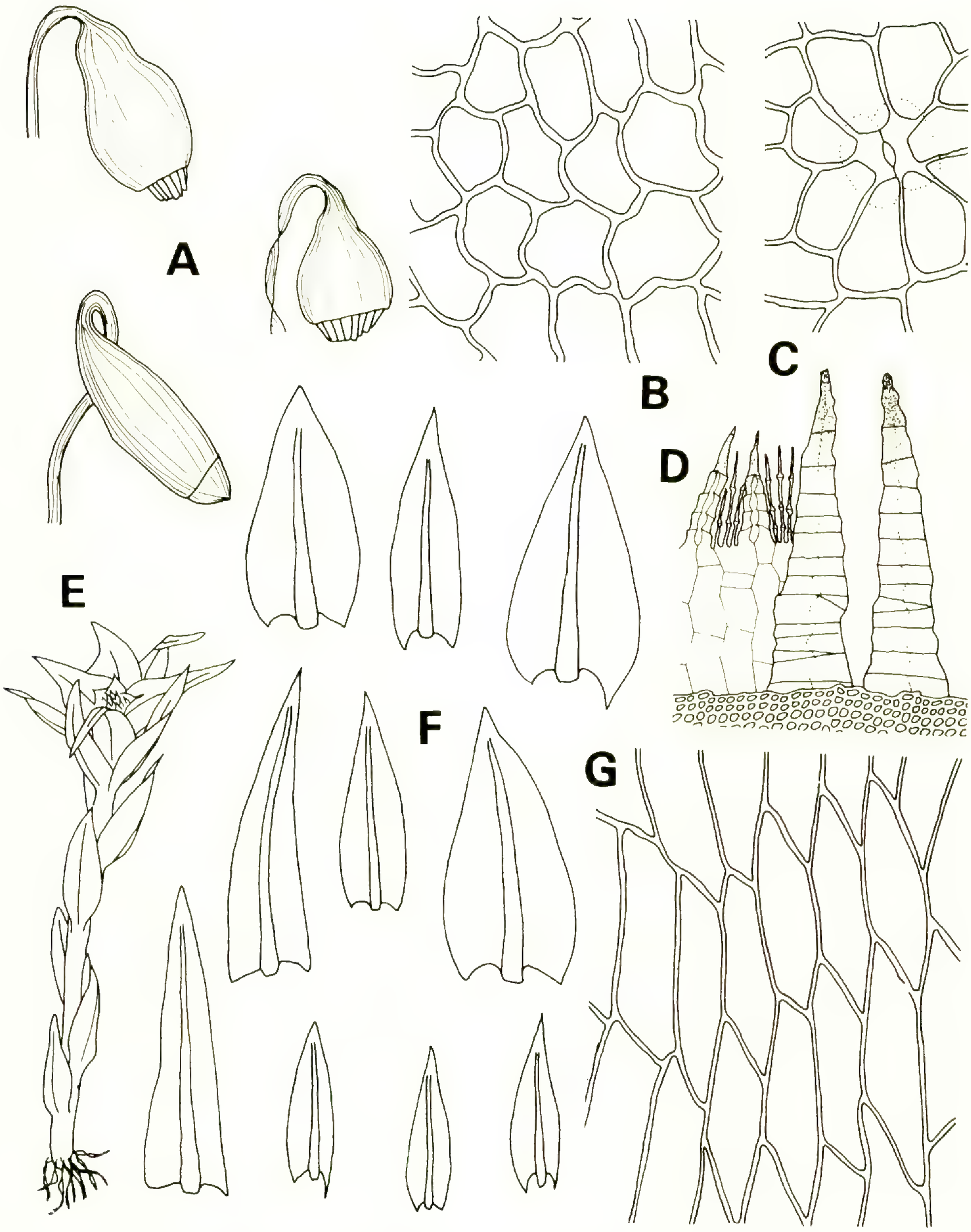


FIG. 28. *Pohlia wahlenbergii*. A. Capsules, ×15. B. Exothecial cells, ×290. C. Stomate, ×290. D. Peristome, ×80. E. Habit, male plant, ×6. F. Leaves, ×22. G. Upper leaf cells, ×290.

bergii may be very slender, with scarcely any superficial resemblance to well-developed forms. The lax cells are helpful in identifying such plants.

Pohlia wahlenbergii, like the following species, produces sporophytes in the spring, and they generally disappear by mid summer. In some areas at least, capsules are abundant in suitably moist sites. All Mexican and Central American collections are sterile.

Small forms may be confused with *P. melanodon*, which is always small but has somewhat glossy, yellow-green leaves that are more acuminate than those of *P. wahlenbergii*. The European *P. wahlenbergii* var. *calcarea* (Warnst.) Warb. is the size of typically well-developed *P. wahlenbergii* but has the gloss and yellowish

leaves of *P. melanodon*. The differences between the var. *calcarea* and typical *P. wahlenbergii* are impressive and warrant further study.

Plants collected by A. Radlow in Baja California (50 mi SW of Mexicali, *8504, 8505,* TENN) are less than one centimeter high, green to reddish-brown, somewhat glossy, and have rhomboidal cells (Fig. 29). They are apparently dioicous, but perigonia or sporophytes are lacking. Although in all liklihood distinct, they are included under *P. wahlenbergii* pending further collections. *Pohlia wahlenbergii* has variably shaped cells but they are almost always broader. Among the *Mniobryums*, *P. longibracteata* and *P. columbica* have cells as narrow as those of the Baja California plants, although in the absence of sporophytes the affinities of the latter is a moot question. The habitat on clay soil along a stream is suggestive of the *Mniobryum* group.

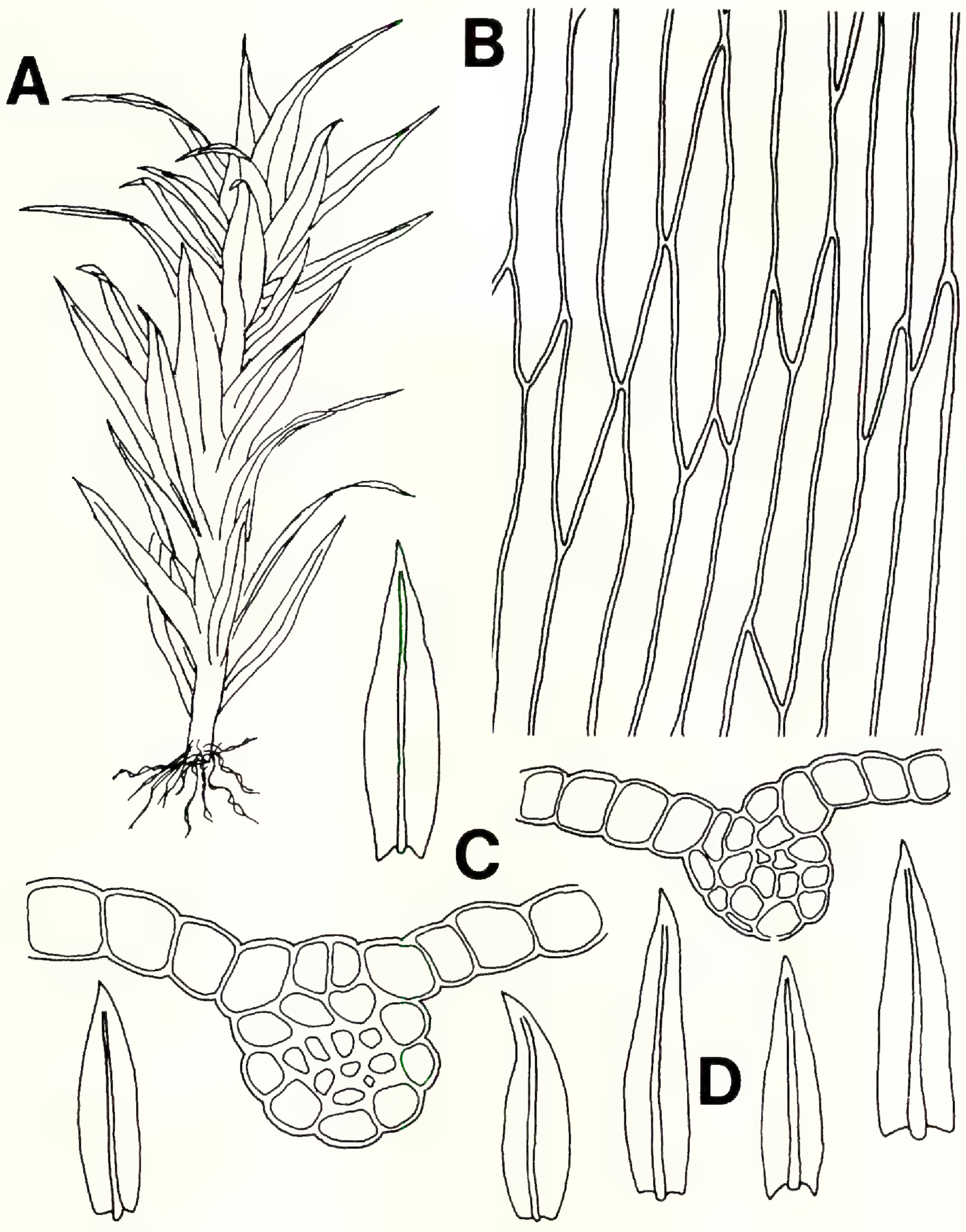


FIG. 29. Plants collected by A. Radlow in Baja California A. Habit, ×30, B. Uppper leaf cells, ×100. C. Costae, transverse sections, ×100. D. Leaves, ×35.

30. **Pohlia melanodon** (Brid.) Shaw, The Bryologist 84: 506. 1982.

Bryum delicatulum Hedw., Spec. Musc. 179. 1801 (type not seen).

Bryum carneum [L. *ex*] With., Syst. Arr. Brit. Pl. ed. 4, 3: 820. 1801 (*nom. illeg. incl. spec. prior.—B. delicatulum*).

Hypnum carneum Web. & Mohr, Ind. Musc. Pl. Crypt. 3. 1803 (*nom. illeg. incl. spec. prior.—B. delicatulum*).

Mnium carneum P. Beauv., Prodr. 74. 1805 (*nom. illeg. incl. spec. prior.—B. delicatulum*).

Bryum melanodon Brid., Bryol. Univ. 1: 845. 1827. (Lectotype: B–Brid.).

Webera carnea Schimp., Coroll. Bryol. Eur. 67. 1855.

Pohlia carnea (Schimp.) Lindb., Musci Scand. 17. 1879.

Webera delicatula (Hedw.) C. Jens., Skand. Bladmfl. 154. 1939.

Pohlia delicatula (Hedw.) Grout, Moss Fl. N. Am. 2: 266. 1940 (*hom. illeg.—P. delicatula* [Mitt.] Broth.).

Slender, glossy, yellow-green plants forming small populations. Stems 2–6 mm, simple when sterile or fertile or rarely with an innovation below perigonia; leaves spreading to erect-spreading, somewhat distant, lanceolate, acute or shortly acuminate, 0.7–1.3 mm long, serrulate near the apex; upper cell laxly and broadly rhomboidal, 60–100 μm long, 10–22 μm wide, somewhat narrower near the margin, with thin walls. Dioicous; perichaetial bracts not strongly differentiated, to 1.9 mm long; perigonial bracts short-acuminate, spreading. Capsules inclined ± 180° from vertical, shortly and broadly pyriform, sometimes urceolate when dry and empty, 1.0–3.0 mm long; exothecial cells isodiametric, ± collenchymatous, 20–45 μm long, with strongly sinuose walls; stomates ± deeply immersed; annuli absent; opercula conic, blunt to acute; exostome teeth dark brown or red-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome yellow to yellow-brown; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 15–22 μm, finely roughened. Fig. 30.

On calcareous clay soil in disturbed, often wet places (ditches, gullies, streambanks, field margins); mostly near sea level. Eastern North America; Ontario and Nova Scotia, New York, New Jersey, Tennessee, Michigan, Ohio and Iowa; Europe; reported from northern Asia; Japan. Sterile specimens from Illinois, Arkansas and Maine probably belong to *P. melanodon*. Map 30.

Exsiccati: Bauer, Musci Eur. Exs. 326 as *M. carneum* (ALTA, BH), 327 as *M. carneum* (ALTA, BH), 1103 as *M. carneum* (ALTA); Erbar, Crittogam Ital. 816 as *W. carnea* (UC); Gyrörffy, Flora Hung. Exs. 929 as *M. carneum* (ALTA, BH, MICH, UC); Harman, Bryac. Scand. Exs. 15 as *W. carnea* (BH); Holmen, Bryoph. Dan. Exs. 152 as *W. delicatula* (ALTA, CAS, UC); Husnot, Musci Gall. 234 as *W. carnea* (BH); Ren. & Card., Musci Eur. Exs. 283 as *W. carnea* (BH); Warnstorf, Märk. Laubm. 173 as *W. carnea* (CAS).

The delicate little plants of *P. melanodon* are best recognized by their glossy yellowish leaves and small capsules with dark-brown exostome teeth, yellow endostomes and deeply sunken stomates. Other than in size and sheen, there is little to distinguish this species from *P. wahlenbergii*, yet the two are rarely confused.

Pohlia melanodon is similar to *P. atropurpurea* and *P. brevinervis*, but the three differ in leaf areolation. In *P. atropurpurea*, the cells of leaves on sterile plants are broad and lax (11–20 μm wide), whereas those of perichaetial bracts are narrow and hexagonal (7–11 μm wide). *Pohlia brevinervis* has narrow, linear cells throughout and *P. melanodon* has lax cells throughout. These differences, though not absolute, help distinguish collections lacking sporophytes (Fig. 32).

Several *Mniobryum* species have exothecial cells just below the rim lax, thin-

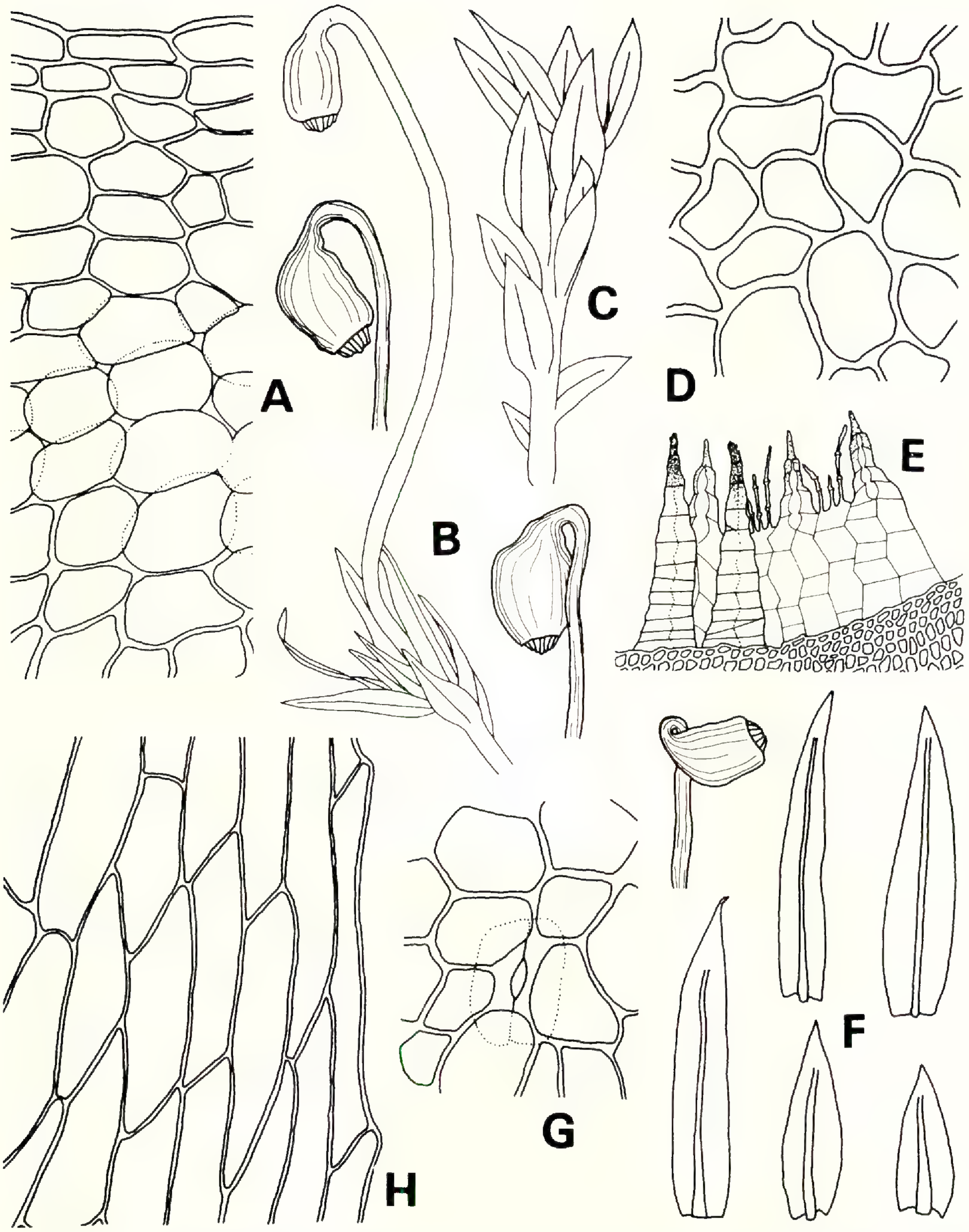


FIG. 30. *Pohlia melanodon*. A. Exothecial cells near the rim, ×290. B. Habit, female plant and capsules, ×8. C. Habit, sterile plant, ×10. D. Exothecial cells, ×290. E. Peristome, ×80. F. Leaves, ×22. G. Stomate, ×290. H. Upper leaf cells showing gradation in shape toward the margin, ×290.

walled and somewhat overlapping (Fig. 30). This is visible under a dissecting microscope as a pale, narrow strip between the urn and rim. It is particularly visible in *P. melanodon* and *P. atropurpurea*, but is also present in such other (non-Mniobryum) species as *P. lescuriana*.

31. **Pohlia atropurpurea** (Wahlenb.) H. Lindb., Acta Soc. F. Fl. Fenn. 16: 14. 1–7. 1899.

Bryum atropurpureum Wahlenb. *ex* Web. & Mohr., Ind. Pl. Crypt. 4. 1803. *nom. nud.*

Bryum pulchellum var. *atropurpureum* Wahlenb., Fl. Lapp. 360. 1812. (Lectotype: S).

B. carneum var. *atropurpureum* (Wahlenb.) Wahlenb., Fl. Lapp. Suppl. 1(2): 91. 1816.

B. atropurpureum (Wahlenb.) Wahlenb. *ex* Fuernr., Flora 12(Ergbl.): 56. 1829.

B. carneum var. *minus* De Not., Syll. 120. 1838 (*nom. illeg. incl. var. prior.—B. carneum* v. *atropurpureum*).

Pohlia borealis Arn. *ex* H. Lindb., Act. Soc. F. Fl. Fenn. 16: 14. 1899 (*nom. nud. in synon.—P. atropurpurea*).

P. arnellii H. Lindb., Act. Soc. F. Fl. Fenn. 16: 14. 1899 (*nom. nud. in synon.—P. atropurpurea*).

P. bardoensis Arn. *ex* H. Lindb., Act. Soc. F. Fl. Fenn. 16: 16:14. 1899 (*nom. nud. in synon.—P. atropurpurea*).

Webera atropurpurea (Wahlenb.) Warnst., Verh. Bot. Ver. Brandenburg 42: 202. 1901.

Mniobryum atropurpureum (Wahlenb.) Hag., Musc. Norv. Bor. 114. 1901.

Webera atropurpurea (Wahlenb.) C. Jens., Skand. Bladmfl. 155. 1939.

Tiny green or reddish plants generally scattered singly with other mosses. Stems 2–6 mm, simple when sterile or fertile. Leaves erect to erect-spreading, distant on sterile stems, overlapping on fertile stems, lanceolate, 0.6–1.3 mm long, serrulate near the apices; upper cells of leaves on sterile plants broadly rhomboidal, 65–110 μm long, 10–15 μm wide, thin-walled, those of the perichaetial bracts narrower (6–11 μm wide). Dioicous; perichaetial bracts ± differentiated, linear-lanceolate, to 3 mm long; perigonial bracts short-acuminate, erect-spreading to spreading. Capsules inclined ± 180° from vertical, shortly pyriform when mature, urceolate when dry and empty, 1.0–2.5 mm long; exothecial cells isodiametric, 15–50 μm long, with strongly sinuose walls; stomates superficial, slightly sunken or ± immersed; annuli lacking; opercula conic, acute; exostome teeth dark brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome yellow to yellow-brown; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 15–21 μm, finely roughened. Fig. 31.

On calcareous, clay soils in wet places (roadbanks, ditches, stream margins), frequently mixed with *P. vexans* and *Bryobrittonia longipes*; low-montane boreal and subarctic habitats, sometimes higher in the mountains. Northern North America; Alaska, Yukon Territory, British Columbia, Washington, Minnesota, Manitoba, Ontario, Iowa, Idaho, and New York; Europe and Asia. Map 30.

Pohlia atropurpurea is characterized by its tiny size, shortly urceolate capsules, almost superficial stomates, dark-brown exostome teeth and yellow endostomes. *Pohlia vexans* is easily separated by its lighter exostome teeth and hyaline endostome.

Although *P. atropurpurea* can be distinguished from *P. melanodon* by several morphological features, the two are obviously closely related. *Pohlia atropurpurea* is a smaller plant and may represent a northern sister species to the more temperate *P. melanodon*. They occupy virtually identical habitats on wet clay soil and when either species grows in the same site with *P. wahlenbergii*, they prefer slightly elevated, presumably drier microhabitats.

32. **Pohlia brevinervis** Lindb. & Arn., Musci Asiae Bor. 51. 1890. (Lectotype: H–SOL).

Webera brevinervis (Lindb. & Arn.) Kindb., Enum. Bryin. Exot. 108. 1891.

Small to very small, whitish, somewhat glossy plants. Stems 2–15 mm, generally simple when sterile or bearing perichaetial, sometimes innovating when bearing perigonia. Leaves erect to erect-spreading, ± crowded and

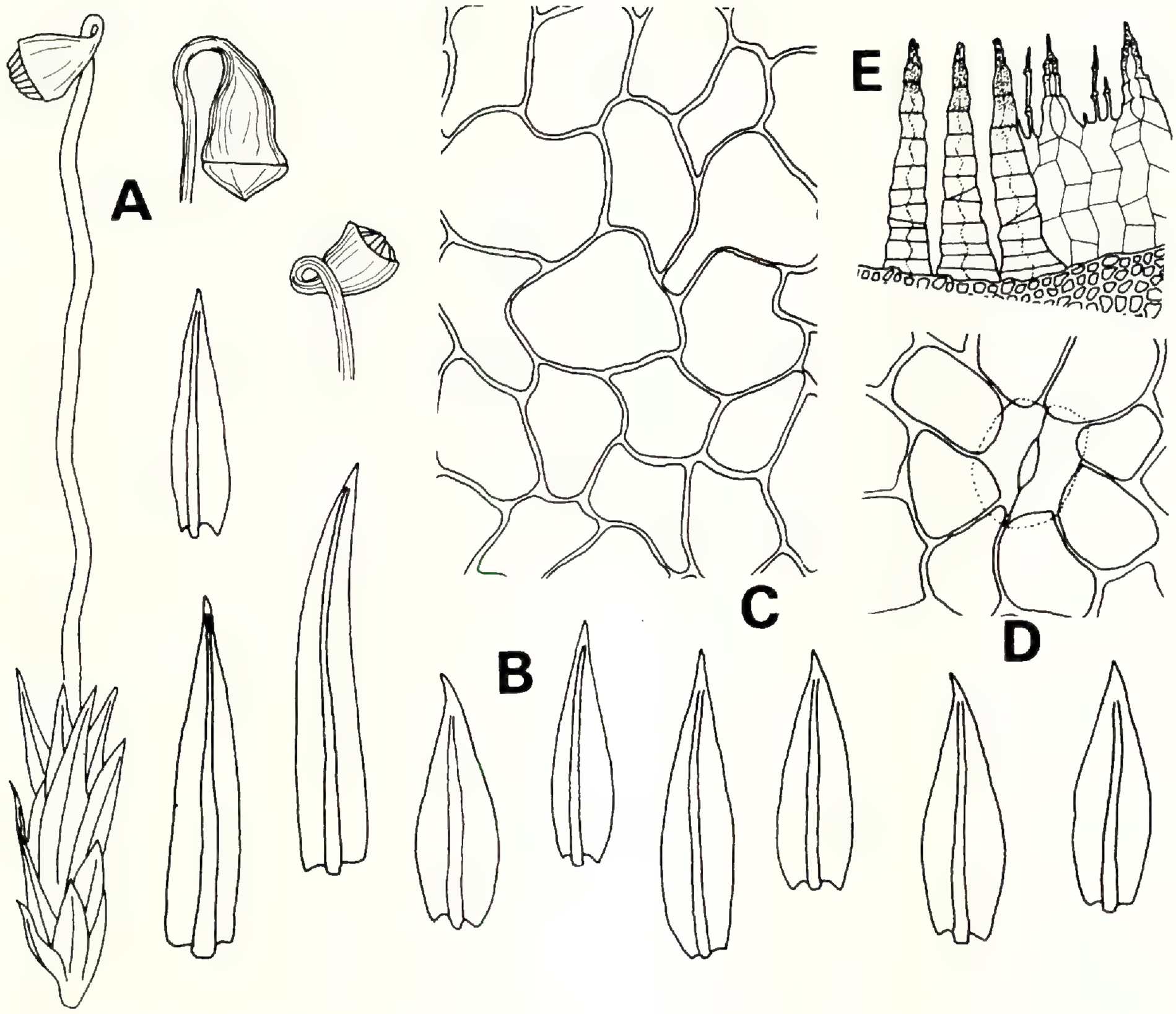


FIG. 31. *Pohlia atropurpurea*. A. Habit, ×12. B. Leaves, ×22. C. Exothecial cells, ×290. D. Stomate, ×290. E. Peristome ×80.

imbricate, lanceolate, 0.7–1.4 mm long, serrulate near the apices; upper cells linear-rhomboidal, 60–110 μm long, 6–9 μm wide, with thin walls. Dioicous; perichaetial bracts slightly differentiated, to 1.9 mm long; perigonial bracts short- to long-acuminate, erect or somewhat spreading. Capsules 150°–180° from vertical, shortly pyriform, 1.0–3.0 mm long; exothecial cells isodiametric, somewhat collenchymatous, 20–40 μm in diameter, with strongly sinuose walls; stomates superficial or somewhat sunken; annuli lacking; opercula conic; exostome teeth dark to light brown or red-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome light yellow; basal membrane slightly more than ½ the exostome length, segments keeled, broadly perforate; cilia long, nodulose. Spores 16–21 μm, finely roughened. Fig. 33.

On clay soil along streams, outwash and other wet places in subarctic and arctic, montane habitats. Western Siberia and northwestern North America (Alaska, Yukon Territory, and Alberta). Map 31.

This very rare species has been collected fewer than ten times. It is known from six localities in western North America, all close to or within areas thought to be ice-free during the last glacial episode.

On the basis of the few specimens available, *P. brevinervis* is distinguished by relatively elongate stems with erect, whitish leaves, dark exostome teeth, yellow endostomes and slightly sunken stomates. The habit of sterile plants resembles *P. vexans* because of the erect, somewhat shiny leaves, but in sporophytic features *P. brevinervis* resembles *P. atropurpurea*.

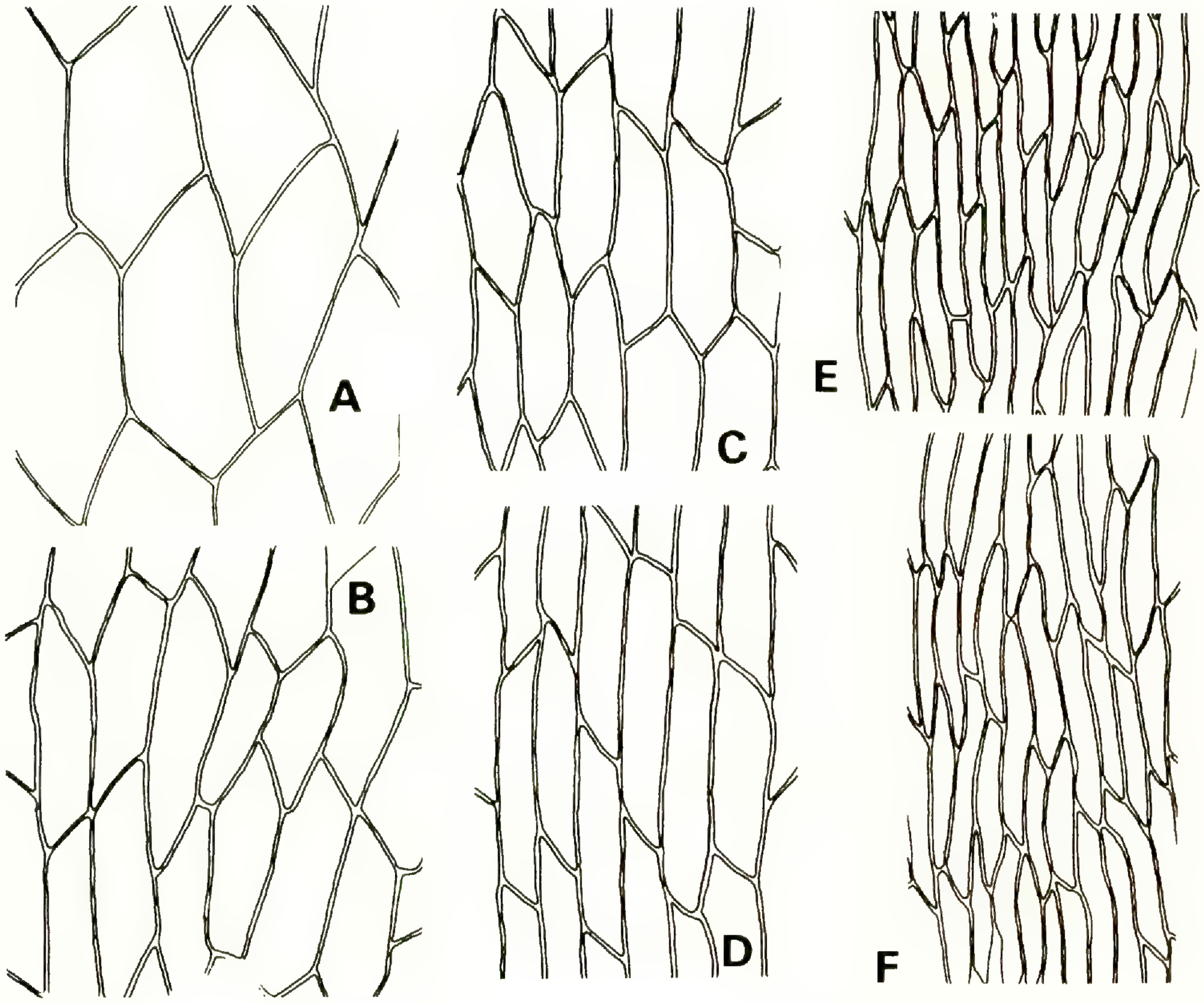


FIG. 32. Upper cells from branch leaves of sterile plants versus perichaetial bracts in "Mniobryum" species, ×260. A–B. *Pohlia melanodon*. A. Branch leaf cells. B. Perichaetial bract. C–D. *Pohlia atropurpurea*. C. Branch leaf. D. Perichaetial bract. E–F. *Pohlia brevinervis*. E. Branch leaf. F. Perichaetial bract.

33. **Pohlia vexans** (Limpr.) H. Lindb., Acta Soc. F. Fl. Fenn. 16: 20. 1899.
Mniobryum vexans Limpr., Laubm. Deutschl. 2: 273. 1892. (Lectotype: BP).
Webera vexans (Limpr.) Par., Ind. Bryol. 1361. 1898.

Slender, glossy plants scattered singly or gregarious, sometimes forming extensive turfs. Stems 5–15 mm, generally simple when fertile or sterile. Leaves erect, imbricate to remote, lanceolate, 0.6–1.3 mm long, serrulate near the apex; upper cells linear-rhomboidal, 70–110 μm long, 6–9 μm wide, with thin walls. Dioicous; perichaetial bracts somewhat differentiated, to 1.8 mm long; perigonial bracts short to long-acuminate, spreading to erect-spreading. Capsules ± 180° from vertical, shortly pyriform, 1.0–3.0 mm long; exothecial cells irregularly isodiametric, 15–45 μm in diameter, with slightly to strongly sinuose, evenly thickened walls; stomates ± deeply immersed, rarely almost superficial; annuli lacking; opercula conic, apiculate; exostome teeth yellow or light brown; acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 17–23 μm, finely roughened. Fig. 34.

Fairly common on calcareous clay soils in wet or moist places (streambanks, roadbanks and other disturbed sites). North-western North America (Alaska, Yukon Territory, Northwest Territories, British Columbia, Alberta, Montana,

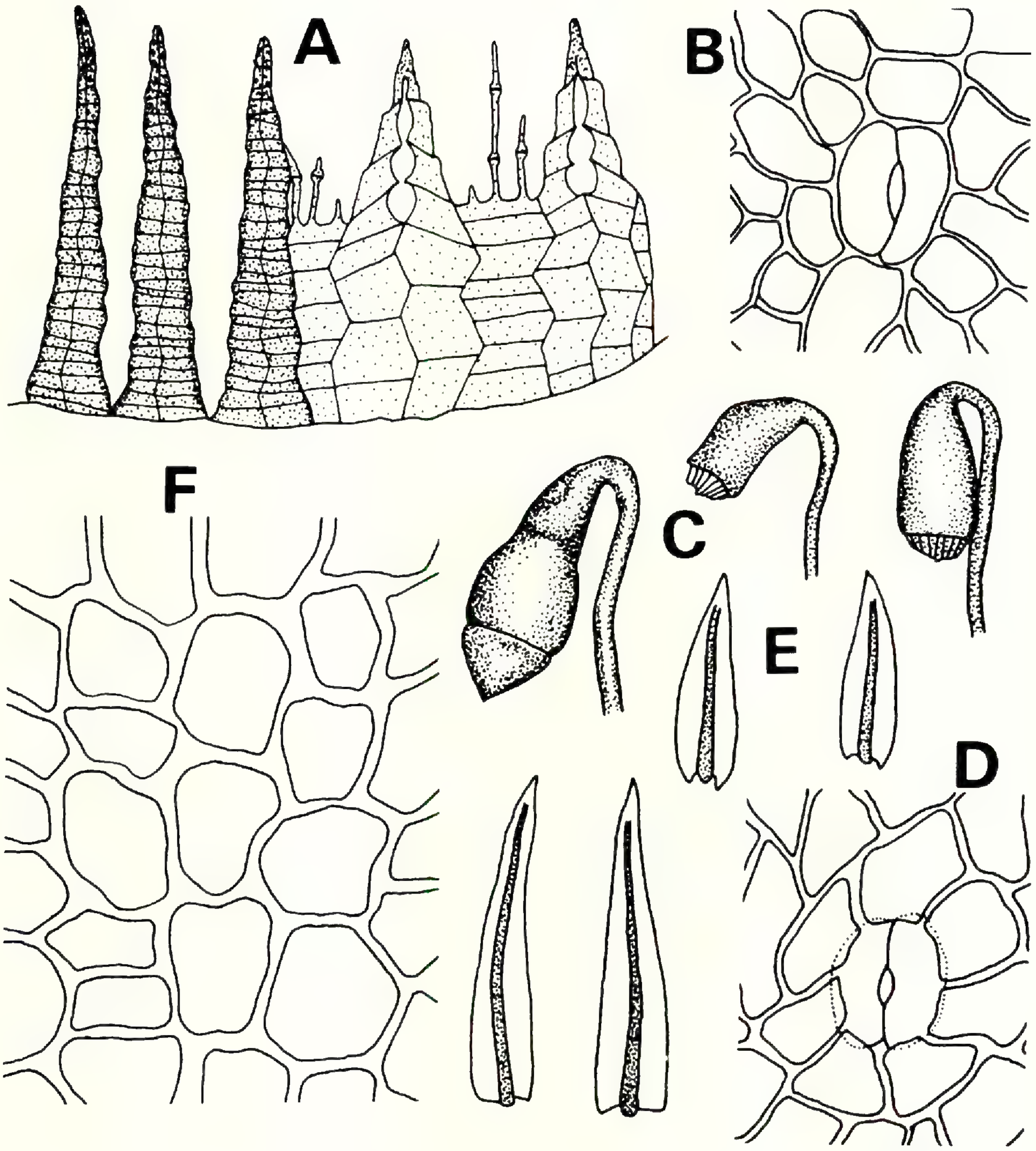


FIG. 33. *Pohlia brevinervis*. (From the Bryologist: in press, 1982) A. Peristome, ×13. B. Stomate, ×490. C. Capsules, ×15. D. Stomate, ×490. E. Leaves, ×33. F. Exothecial cells, ×490.

Manitoba); northern and central Europe; reported from northern Asia by Crundwell and Nyholm (1977). The dot map showing the distribution of this species obviously represents collection localities along the Alaska Hwy. rather than the actual distribution of *P. vexans* populations. Map 32.

Exsicatti: Bauer, Musci Eur. Exs. 328 as *M. vexans* (BH), 1628 as *M. vexans* (WTU); Husnot, Musci Gall. 826 as *W. lutescens* (BH); Macoun, Flora Canadensis 628a as *B. pulchellum* (CANM).

Pohlia vexans is best recognized by erect, glossy leaves on a red stem (at least when moist). It is more common than *P. atropurpurea* and *P. brevinervis*, occurring along many of the sizable streams with clay banks in Alberta, British Columbia and the Yukon. It is restricted to soils of high pH, 6.5 or above.

34. **Pohlia columbica** (Kindb. *in* Macoun & Kindb.) Andr. *in* Grout, Moss. Fl. N. Am. 2: 202. 1935.
Webera columbica Kindb. *in* Macoun & Kindb., Cat. Canad. Pl. 6: 115. 1892.

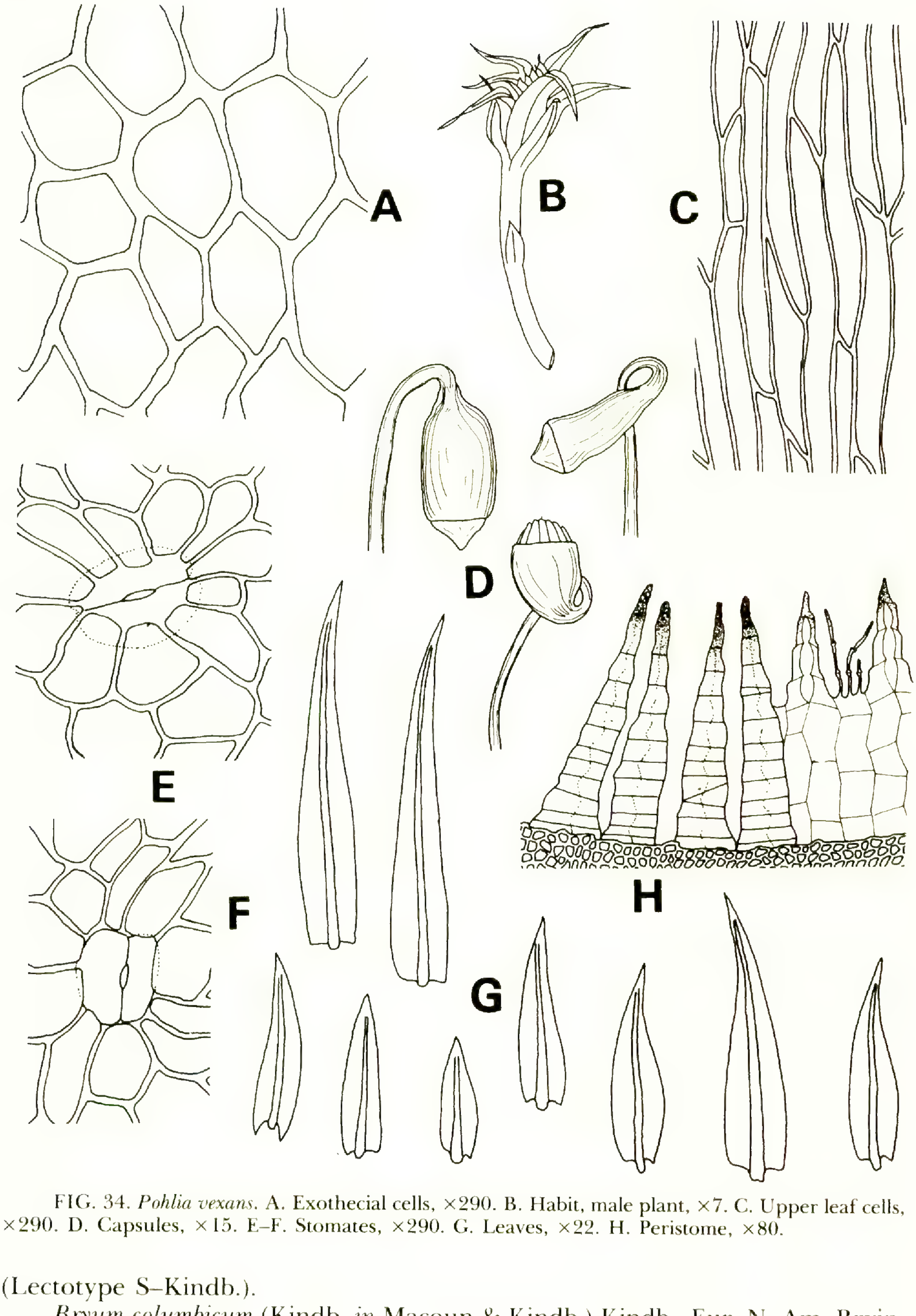


FIG. 34. *Pohlia vexans*. A. Exothecial cells, ×290. B. Habit, male plant, ×7. C. Upper leaf cells, ×290. D. Capsules, ×15. E–F. Stomates, ×290. G. Leaves, ×22. H. Peristome, ×80.

(Lectotype S–Kindb.).

Bryum columbicum (Kindb. *in* Macoun & Kindb.) Kindb., Eur. N. Am. Bryin. 2: 386. 1897.

Pohlia decurrens H. Lindb., Act. Soc. F. Fl. Fenn. 16: 12. 1899. (*nom. illeg. incl. spec. prior.—W. columbica*).

Mniobryum columbicum (Kindb. *in* Macoun & Kindb.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

Slender, green or reddish, rather dull plants. Stems 4–8 mm, simple when sterile or fertile. Leaves erect-spreading or spreading, rather distant, narrowly

lanceolate to lanceolate, 1.4–2.5 mm long, serrate near the apex or to midleaf; upper cells linear-hexagonal, 85–150 μm long, 6–10 μm wide, with thin walls. Dioicous; perichaetial bracts ± differentiated, linear-lancelate, to 3.0 mm long; perigonial bracts rather long-acuminate, wide-spreading. Capsules inclined 100°–180° from vertical, broadly pyriform or urceolate, 1.5–3.5 mm long; exothecial cells isodiametric, somewhat collenchymatous, 20–40 μm in diameter, with strongly sinuose walls; stomates immersed; annuli lacking; opercula conic, acute; exostome teeth yellow or light brown, acuminate, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline or very pale yellow; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 13–18 μm, nearly smooth. Fig. 35.

Very rare; on soil in disturbed places and along streams; mostly near sea level along the Pacific Coast. Apparently endemic to coastal Alaska, British Columbia and Washington. Map 33.

This species is close to *P. longibracteata* but is distinguished by its duller, often reddish leaves, and less conspicuously long perigonial bracts. Whereas *P. longibracteata* is common along the Pacific coast, *P. columbica* is exceedingly rare. I have had no success finding it at the type locality or elsewhere near the coast, although W. B. Schofield has collected it in several places in British Columbia.

The Japanese *P. fauriei* (Card.) Ochi, including *Webera densiretis* Broth., is a rather puzzling, variable intermediate between *P. columbica* and *P. longibracteata*, but according to Ochi (1959) distinct from both. Shiny plants of *P. fauriei* that look like compact expressions of *P. longibracteata* lack the diagnostic very long perigonial bracts. This small complex of the three closely related species is of some phytogeographic interest since they are endemic to the North Pacific region.

35. **Pohlia longibracteata** Broth. *in* Roell, Bot. Centralbl. 44: 419. 1890. (Lectotype: H–SOL).

Webera longibracteata (Broth. *in* Roell) Ren. & Card., Rev. Bryol. 19: 66. 1892.

Bryum longibracteatum (Broth. *in* Roell) Kindb., Eur. N. Am. Bryin. 2: 384. 1897.

Webera lachenaudii Card. & Thér. *in* Bailey, Bryologist 7: 66. 1904. (Isotype: BH, CANM, UC).

Robust, shiny plants forming small populations. Stems 5–25 mm, generally simple when sterile or fertile. Leaves wide-spreading, narrowly and longly lanceolate, distant to crowded, 2–3.5 mm long, rather coarsely serrate near the apices; upper cells linear-hexagonal, 80–160 μm long, with thin walls. Dioicous; perichaetia terminal, or on short, axillary branches; perichaetial bracts ± differentiated, to 4 mm long; perigonia terminal or on short, axillary branches; perigonial bracts extremely long-acuminate, to 6 mm long, wide-spreading. Capsules inclined ± 180° from vertical, broadly pyriform to urceolate, 1.5–3 mm long; exothecial cells isodiametric, 20–40 μm in diameter, with straight to sinuose walls; stomates immersed; annuli lacking; opercula shortly to longly and obliquely rostrate; exostome teeth light-brown to yellow, acuminate, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane slightly more than ½ the exostome height; segments keeled, broadly perforate; cilia long, nodulose. Spores 14–20 μm, almost smooth. Fig. 36.

Fairly common on calcareous, neutral or mildly acidic soils in wet, often disturbed places at sea level (ditches, gullies, roadbanks, stream margins).

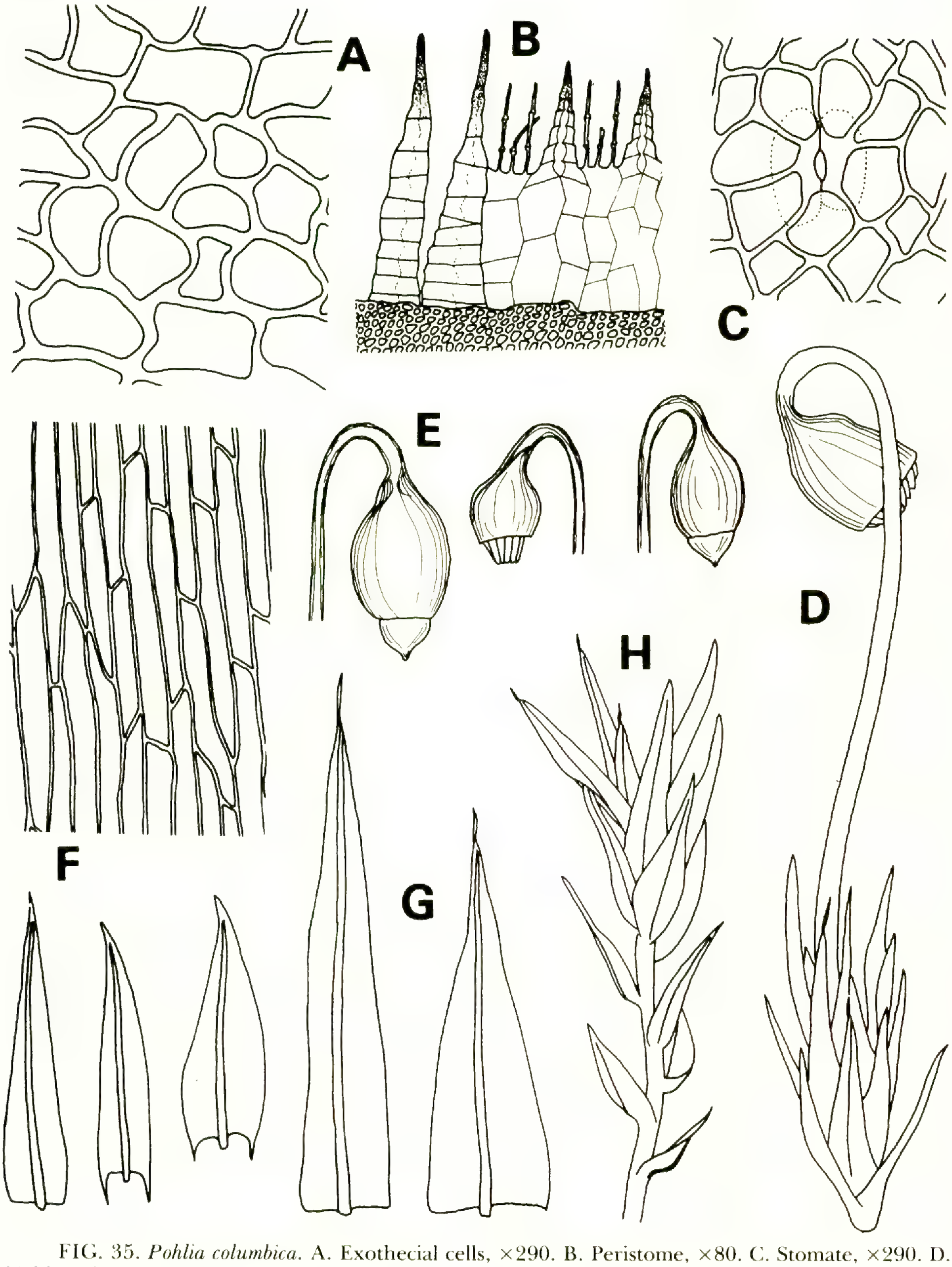


FIG. 35. *Pohlia columbica*. A. Exothecial cells, ×290. B. Peristome, ×80. C. Stomate, ×290. D. Habit, ×9. E. Capsules, ×15. F. Upper leaf cells, ×290. G. Leaves, ×22. H. Habit, sterile plant, ×9.

Endemic to western North America; British Columbia, Washington, Oregon and California (south to Santa Clara Co.). Map 34.

Exsiccati: Grout, N. Am. Musci Perf. 135 as *M. albicans* (MICH); Holzinger, Musci Acro. Bor.–Am. 95 as *W. lachenaudii* (BH, CANM, UC).

Our only common *Pohlia* along the coast of California, Oregon and Washington, *P. longibracteata* is striking because of its large size and very glossy leaves. It is most common along roadsides in wet ditches, but can also be found in undisturbed sites such as muddy streambanks in Redwood forests. The name refers to the perigonial bracts, which are very conspicuous, reaching six millimeters in length.

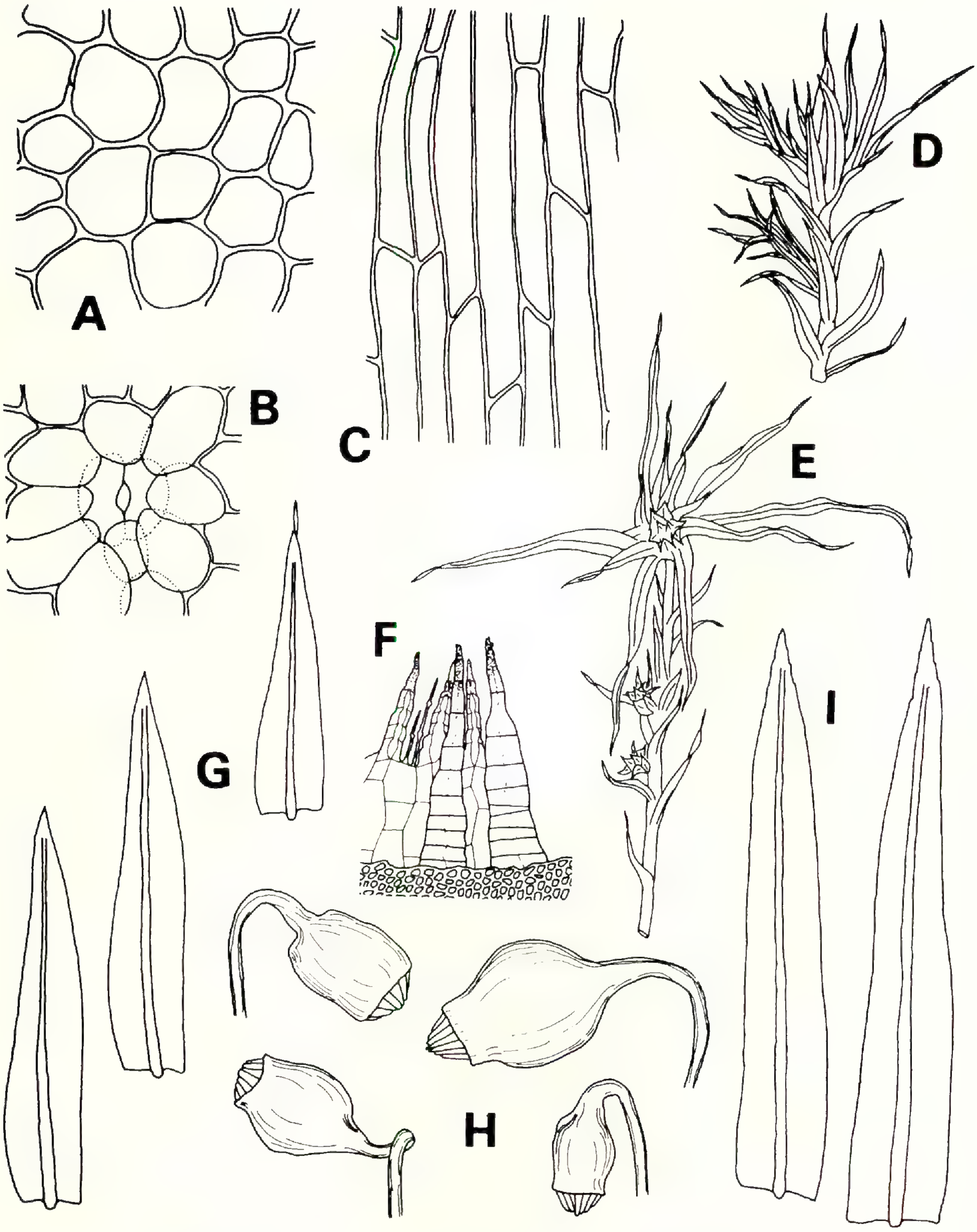


FIG. 36. *Pohlia longibracteata*. A. Exothecial cells, ×290. B. Stomate, ×290. C. Upper leaf cells, ×290. D. Habit, female plant with perichaetia terminal and on short axillary branches, ×4. E. Habit, male plant with terminal and axillary perigonia, ×4. F. Peristome, ×80. G. Leaves, ×22. H. Capsules, ×15. I. Perichaetial bracts, ×22.

It is an interesting feature of *P. longibracteata* that although the inflorescences are generally terminal, it is not uncommon to find them also on short, axillary branches (Fig. 36). Such lateral inflorescences are of the same sex as those that are terminal on the main stem. I have not found any autoicous plants.

36. **Pohlia integra** (Card.) Shaw, comb. nov.

Webera integra Card., Rev. Bryol. 38: 4. 1911. (Isotypes: BH, BM, MO, US).

Mniobryum integrum (Card.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 362. 1924.

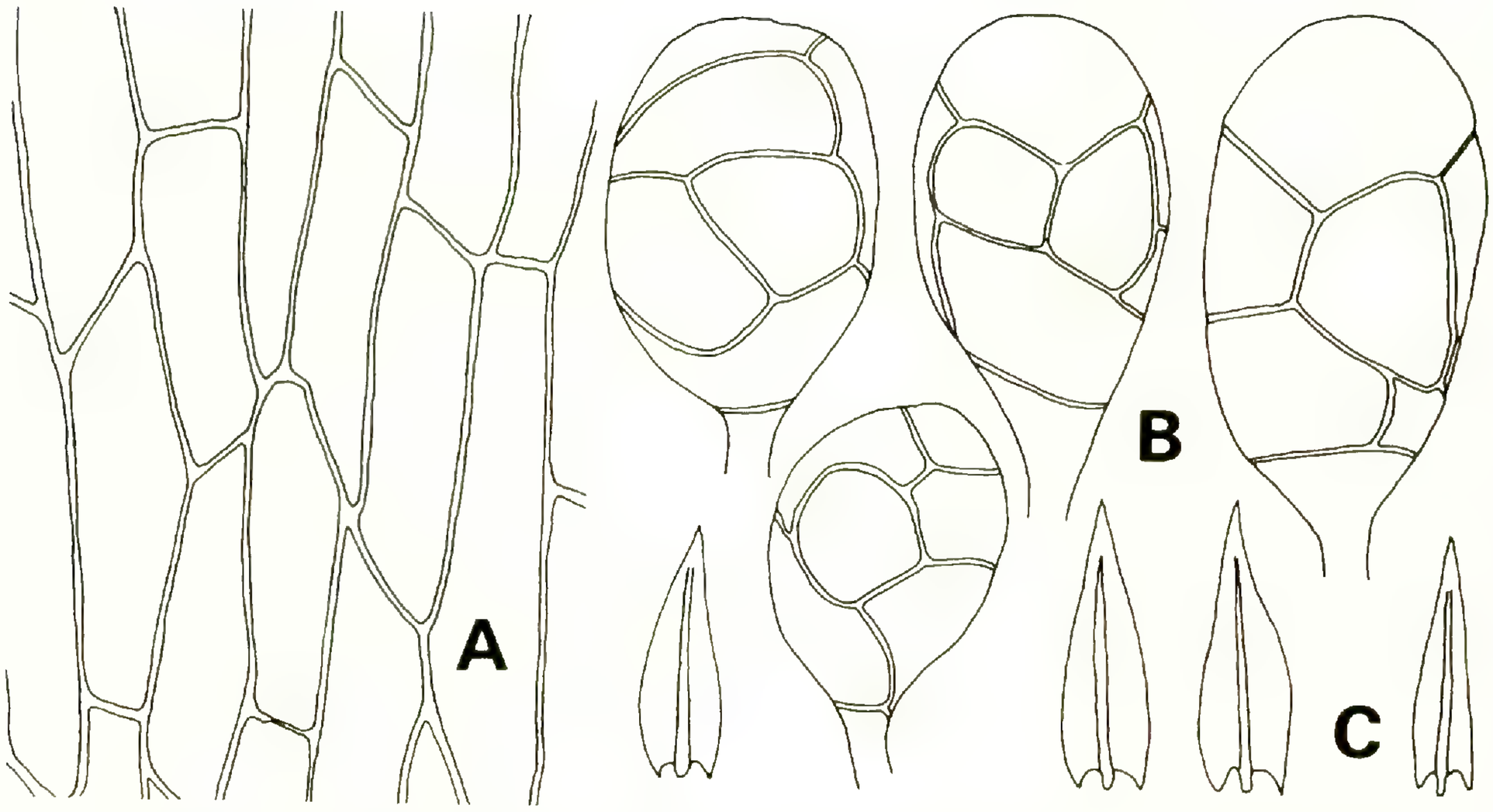


FIG. 37. *Pohlia integra*. A. Upper leaf cells, ×290. B. Rhizoidal tubers, ×200. C. Leaves, ×22.

Very small, pale green to yellow-green, glossy plants. Stem up to 28 mm high, simple. Leaves delicate, flexuose when dry, rather distant, 0.6–1.3 mm long, entire to crenulate near the apices; upper cells laxly elongate-hexagonal, 70–140 μm long, 13–20 μm wide, with thin walls. Gemmae abundant on matted rhizoides at the stem base, also present but infrequent on single rhizoids in the leaf axils, round or more commonly oblong, red-brown, 140–240 μm in the longest dimension; consisting of about 10–14 ± isodiametric cells, each about 90 μm in diameter, the superficial cells not bulging. Inflorescences and sporophytes unknown. Fig. 37.

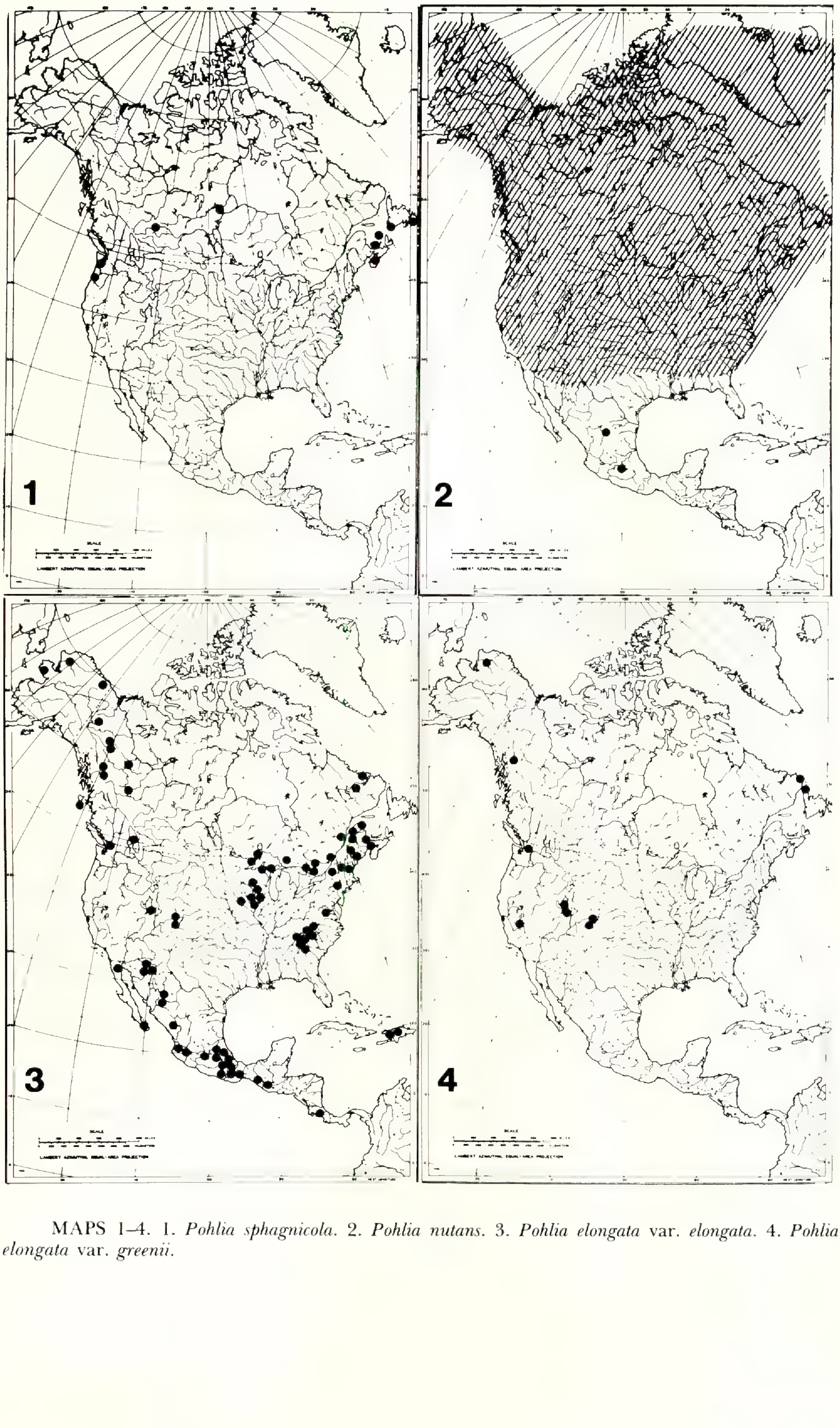
On calcareous clay in rock crevices; endemic to central Mexico (Ixtaccíhuatl). Map 35.

Although *P. integra* is known only from the type locality, the original specimen must have been copious for isotypes are present in a number of herbaria. I have not seen a specimen from the Cardot herbarium in Paris, but since the type material seems to be uniform it would be surprising if such a specimen differs significantly from others.

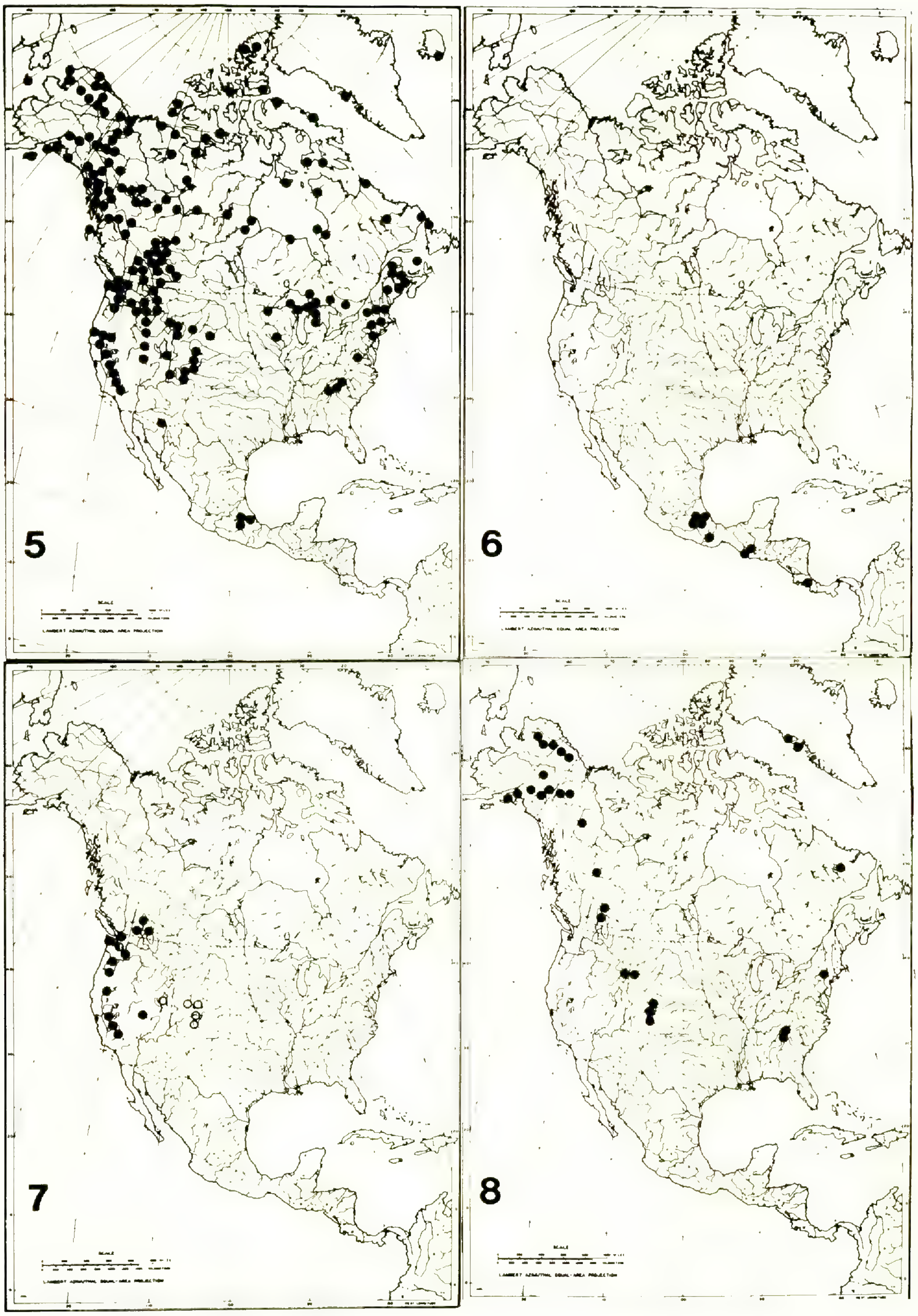
Although sterile, a relationship to the previous "Mniobryum" species is indicated by the lax leaf cells. *Pohlia integra* is distinguished most readily by abundant, deep red, rhizoidal tubers. Compared to *P. wahlenbergii*, which also occurs in central Mexico, *P. integra* has more yellowish, glossy leaves.

DOUBTFUL TAXA

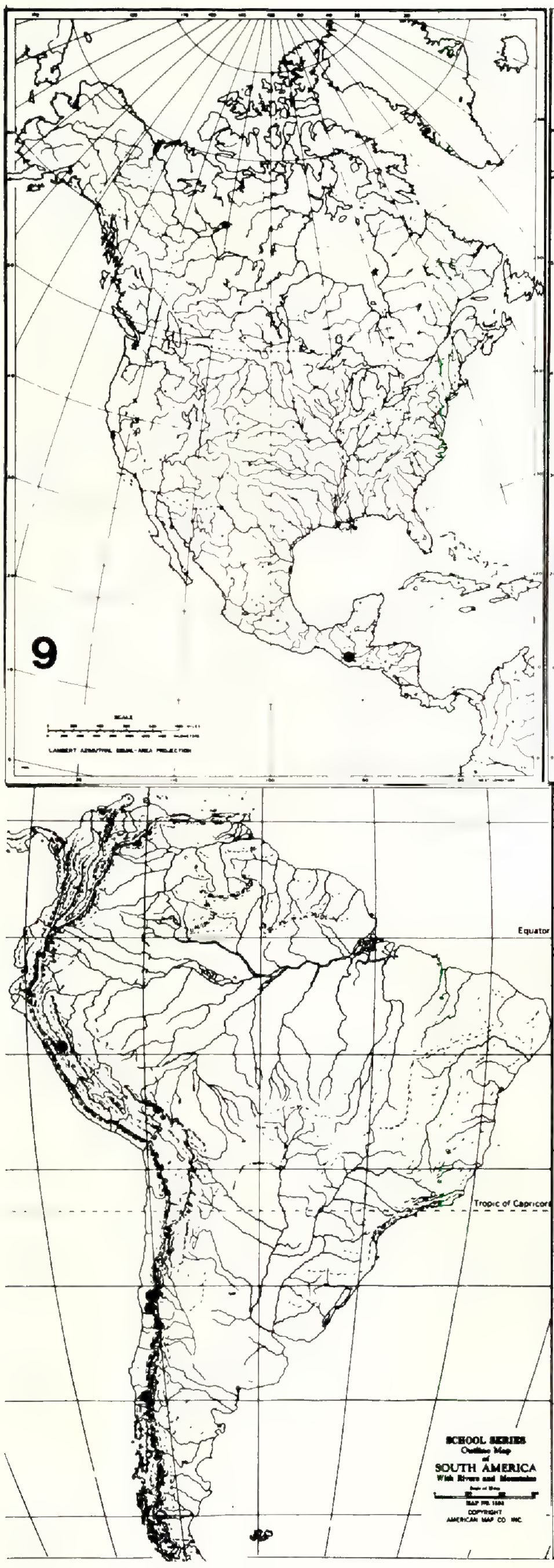
Type specimens for a relatively extensive list of species described by Hoppe and Hornschuch and other early authors were not available for study. Such early names could prove important if types are found in the future. *Webera microapiculata* C. Müll. & Kindb. *in* Macoun, Cat. Canad. Pl. 6: 115. 1892: A type for this species is in the Kindberg herbarium. It is dioicous, lacks sporophytes, and has erect, somewhat glossy leaves. Although it does not agree with any of the species included here, it hardly seems distinctive enough to recognize at present. Only additional collections will help distinguish it as a good species rather than an aberrant form of something else, perhaps *P. cruda*.

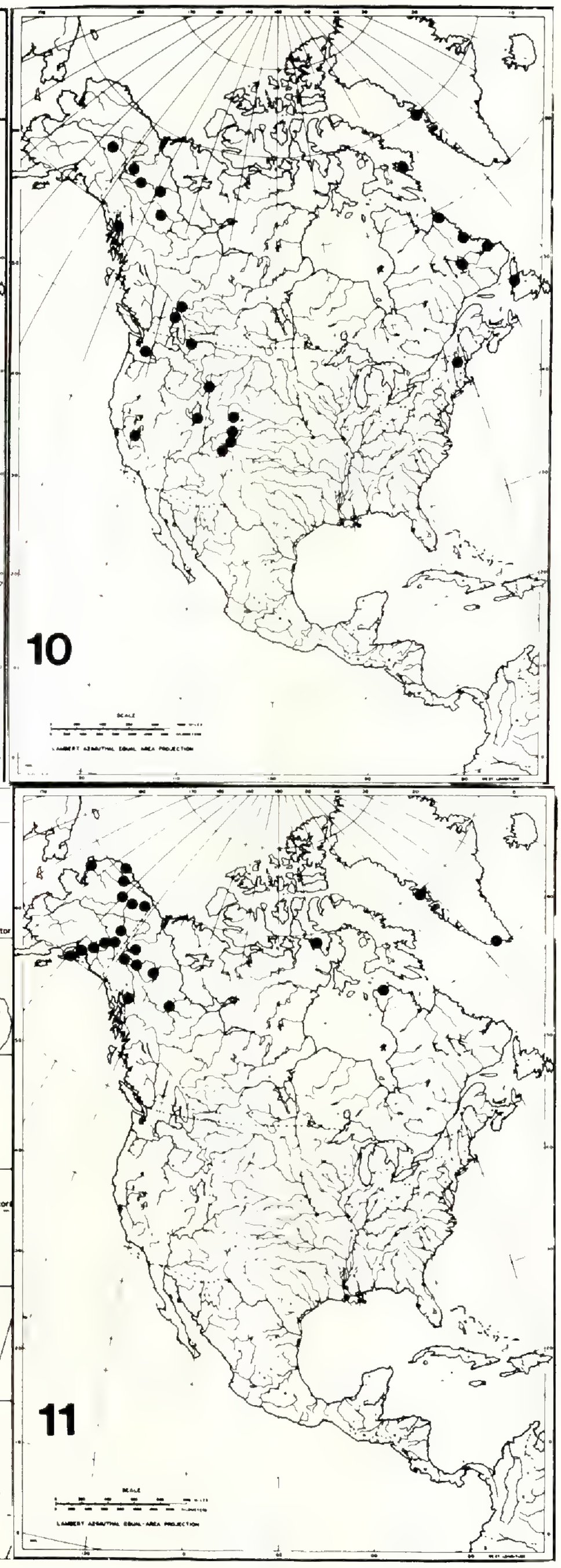


MAPS 1–4. 1. *Pohlia sphagnicola*. 2. *Pohlia nutans*. 3. *Pohlia elongata* var. *elongata*. 4. *Pohlia elongata* var. *greenii*.



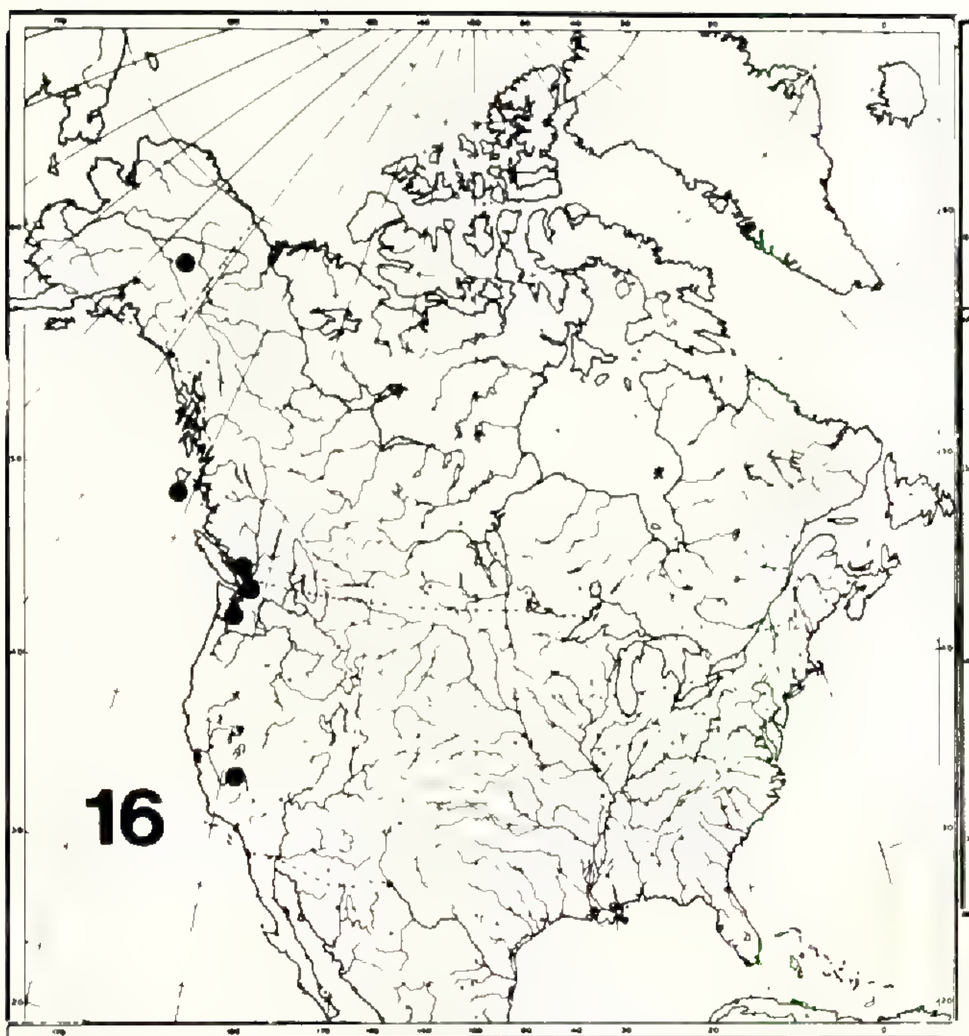
MAPS 5–8. 5. *Pohlia cruda*. 6. *Pohlia oerstediana*. 7. *Pohlia bolanderi* var. *bolanderi* (solid circles) and var. *seriata* (hollow circles). Half black circles on Mt. Rainier, Washington marks an area of sympatry. 8. *Pohlia longicollis*.

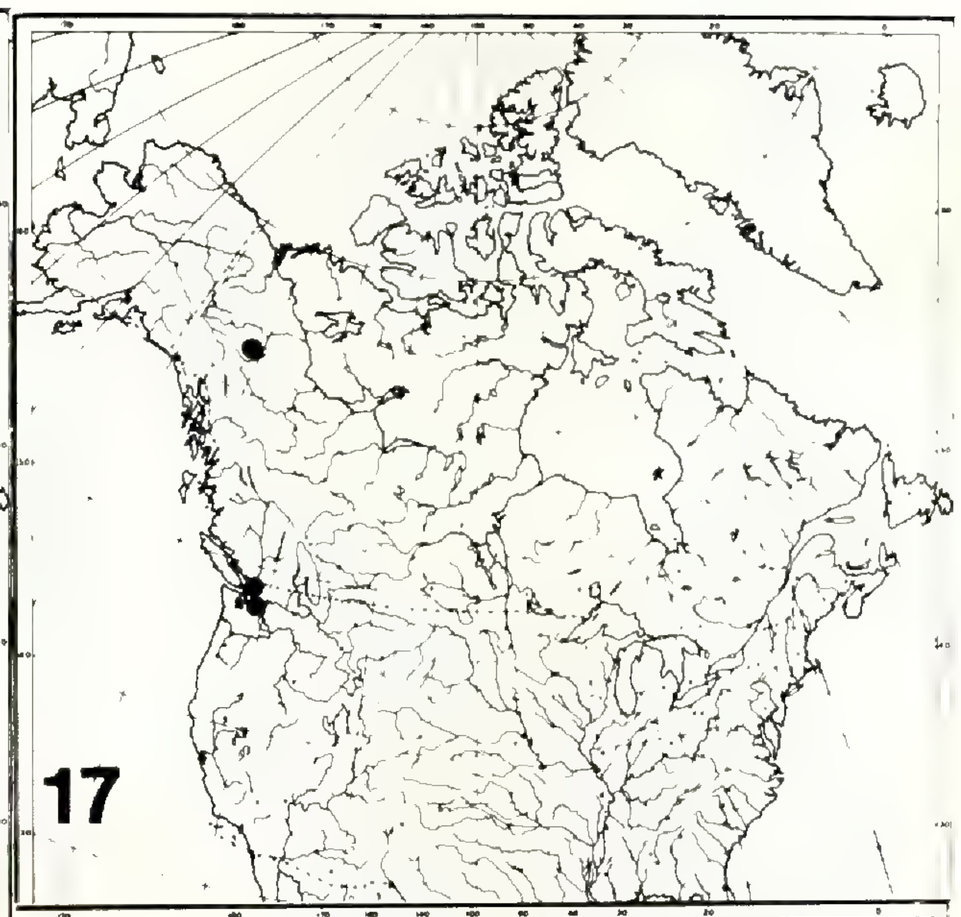


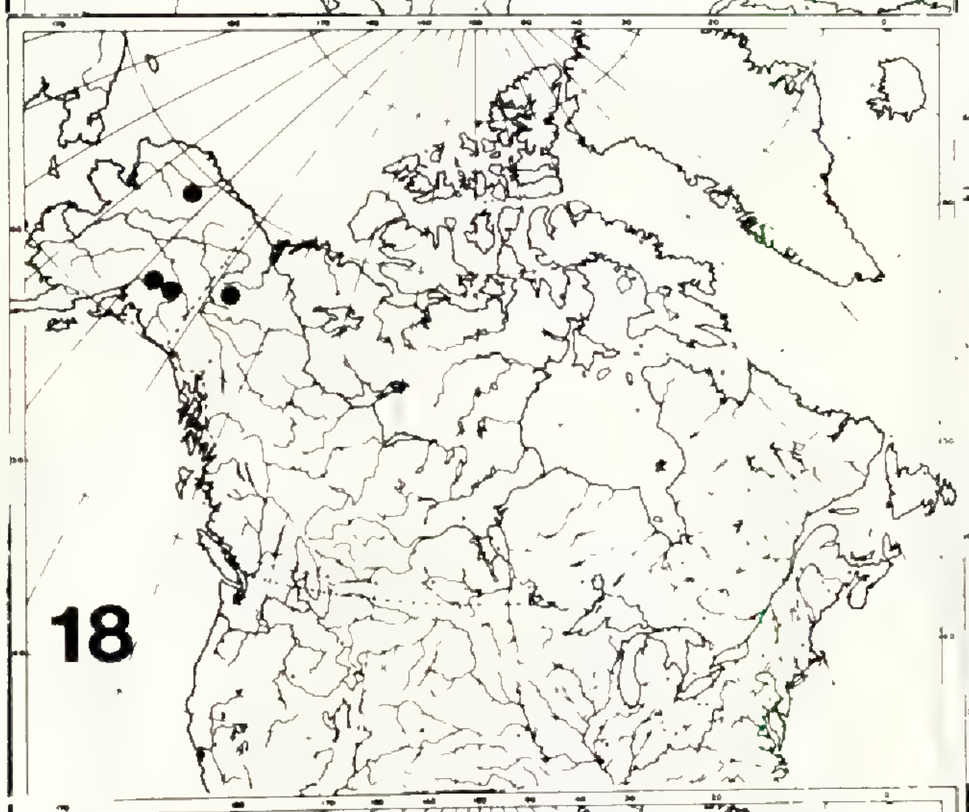


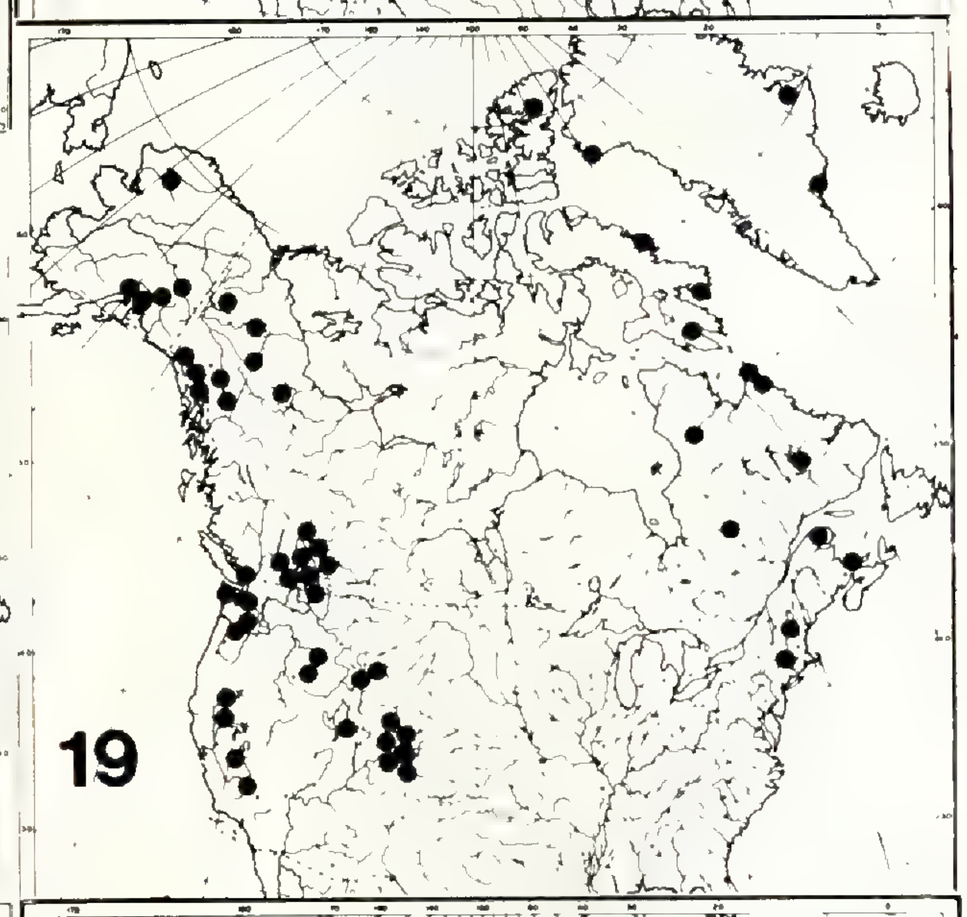
MAPS 9–11. 9. *Pohlia polycarpa*. 10. *Pohlia obtusifolia*. 11. *Pohlia crudoides*.

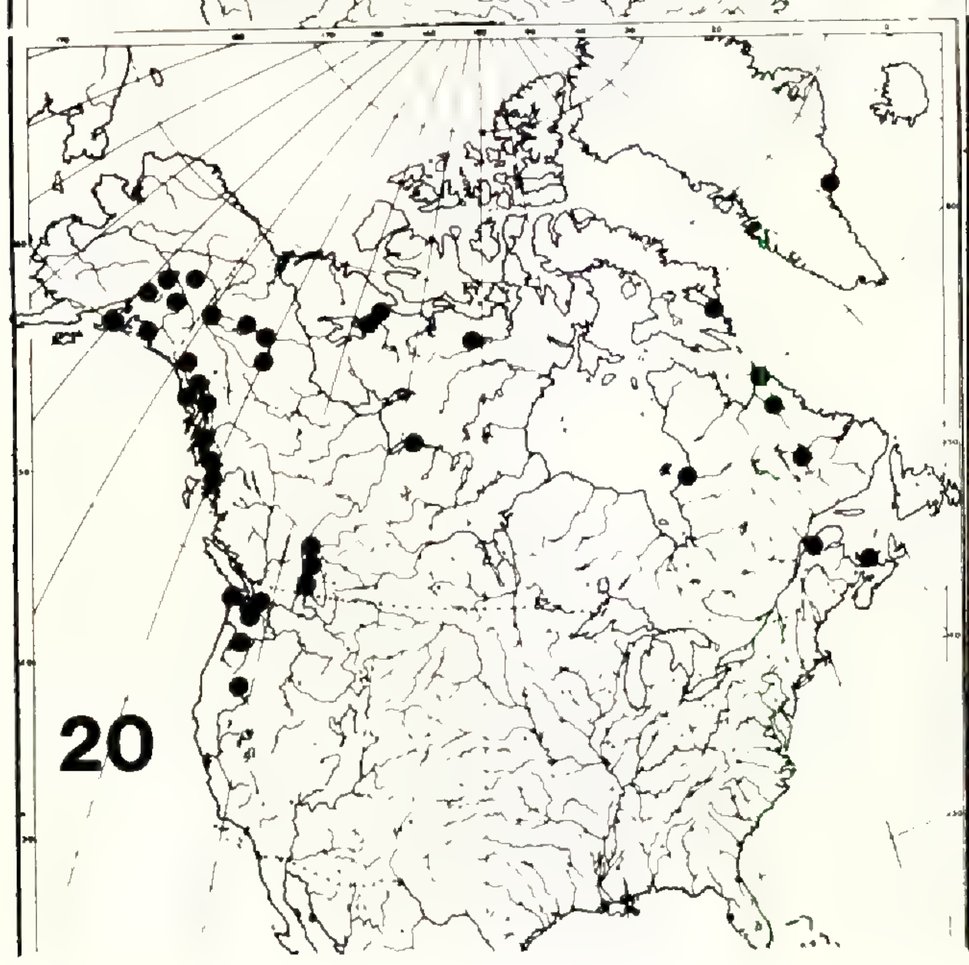
MAPS 12–15. 12. *Pohlia papillosa*. 13. *Pohlia richardsii*. 14. *Pohlia pseudo-barbula*. 15. *Pohlia ludwigii*.

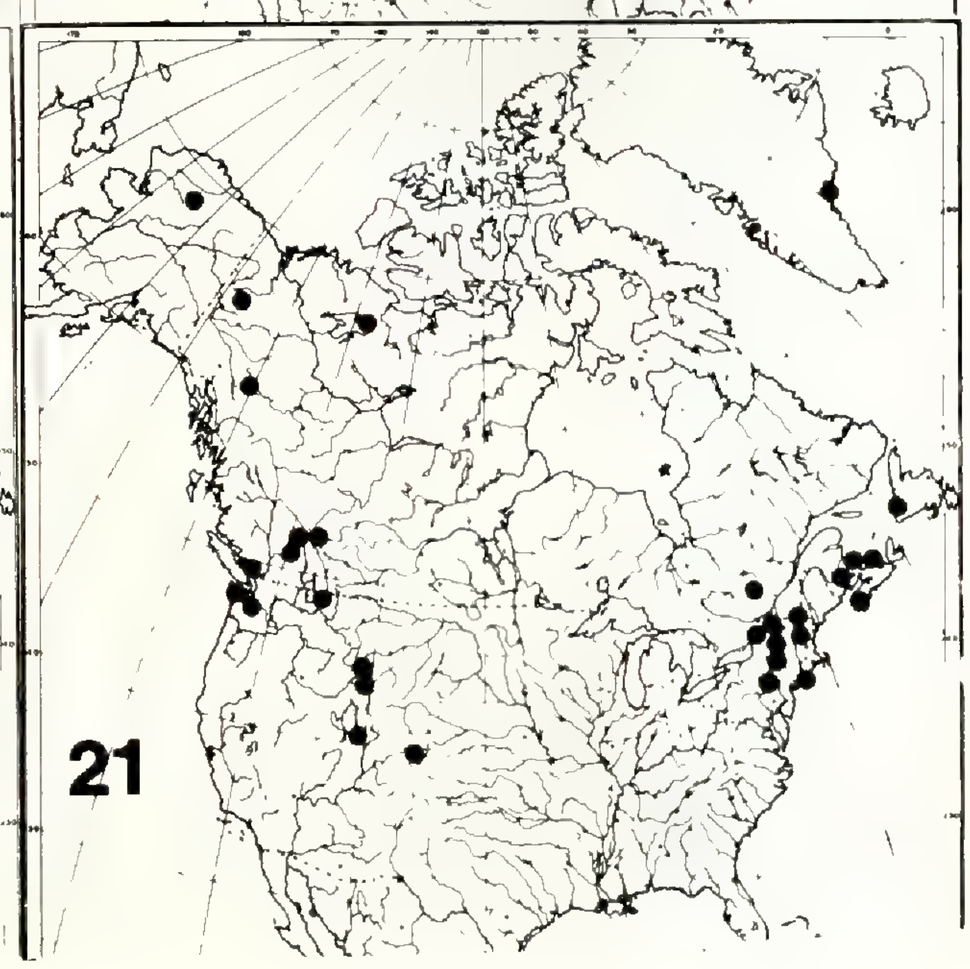




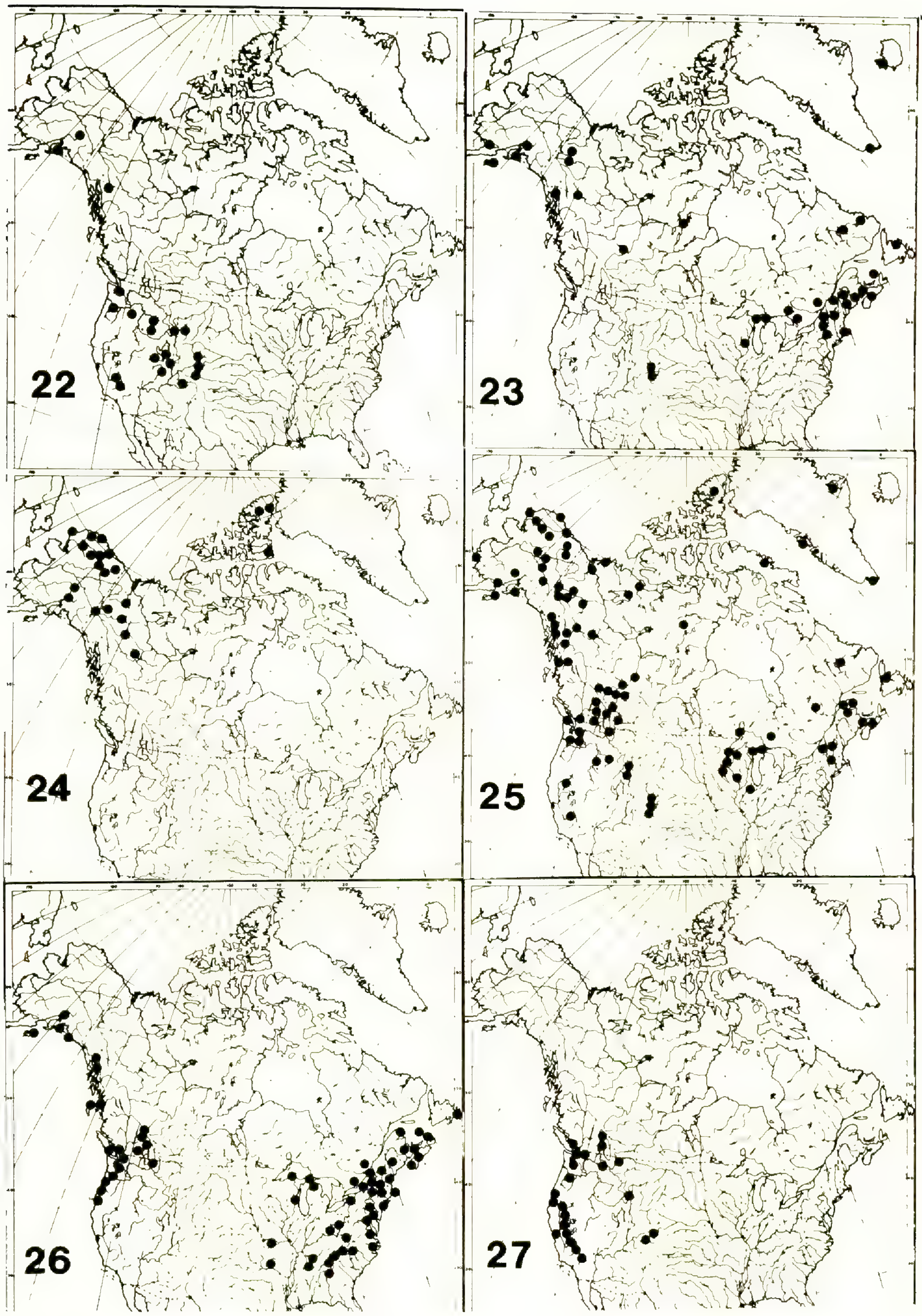




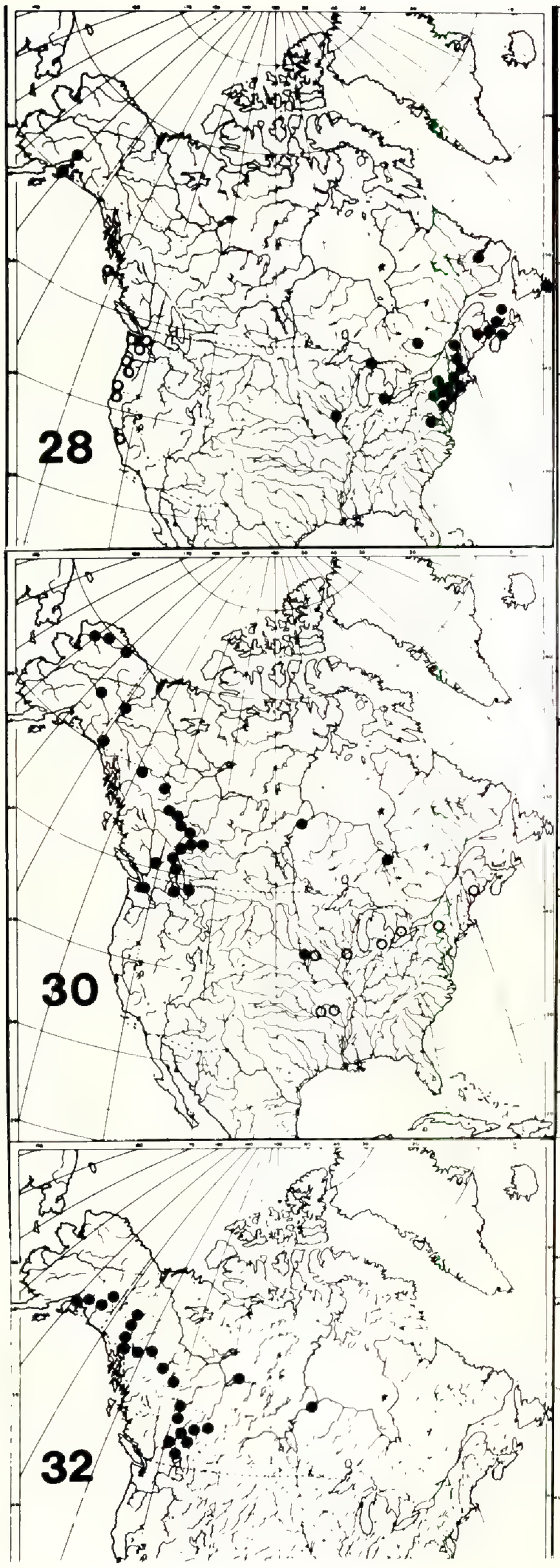


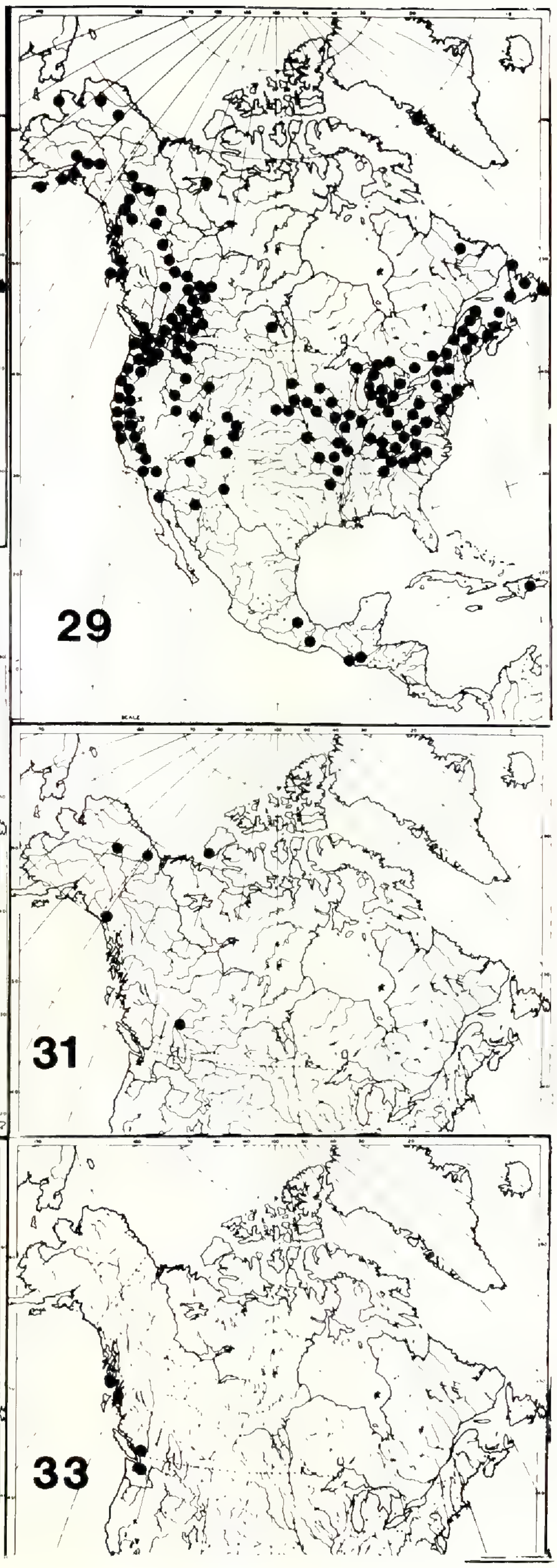


MAPS 16–21. 16. *Pohlia cardotii*. 17. *Pohlia erecta*. 18. *Pohlia beringiensis*. 19. *Pohlia drummondii*. 20. *Pohlia filum*. 21. *Pohlia andalusica*.

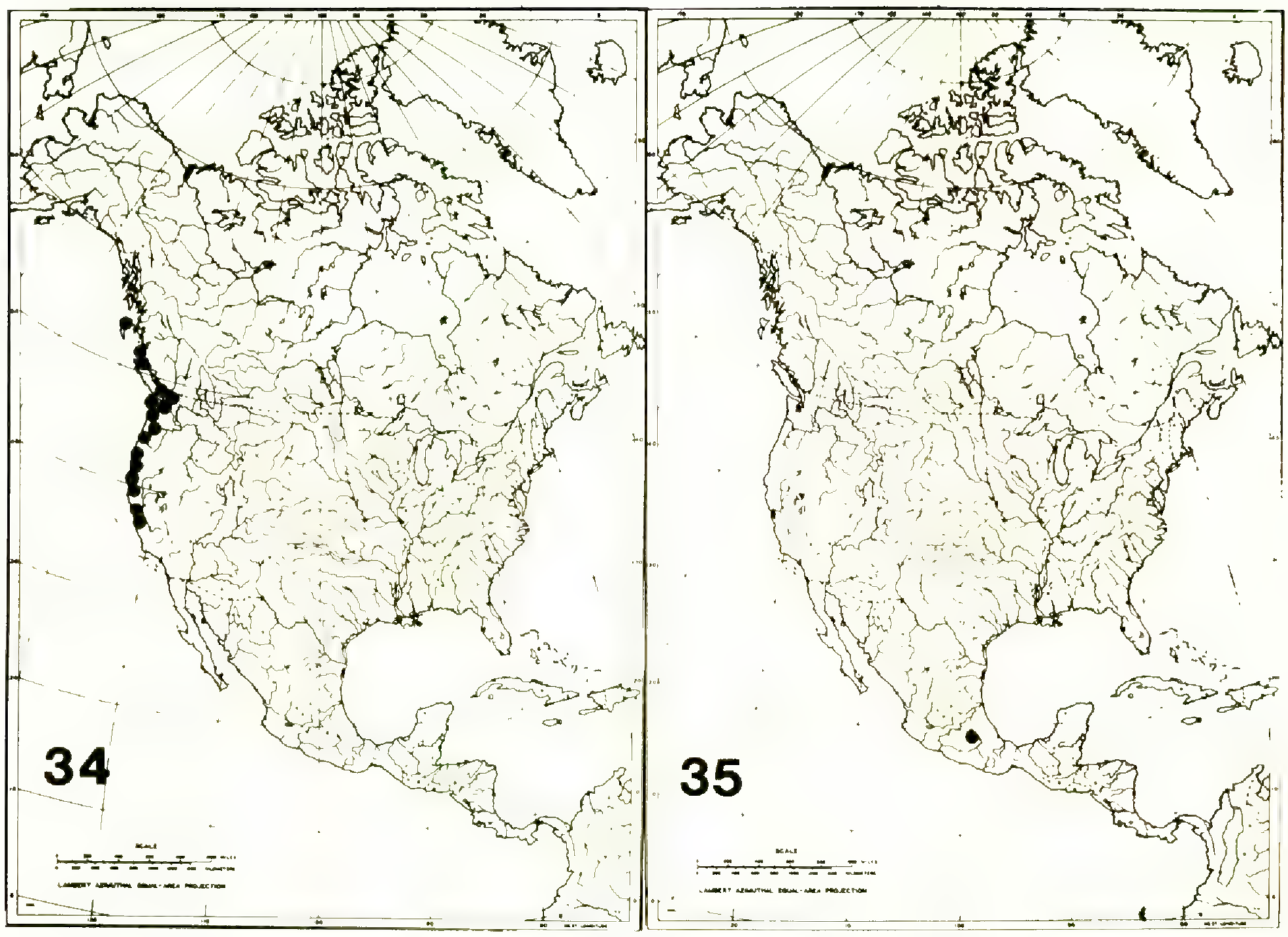


MAPS 22–27. 22. *Pohlia tundrae*. 23. *Pohlia bulbifera*. 24. *Pohlia andrewsii*. 25. *Pohlia proligera*. 26. *Pohlia annotina*. 27. *Pohlia camptotrachela*.





MAPS 28–33. 28. *Pohlia pacifica* (hollow circles) and *Pohlia lescuriana* (solid circles). 29. *Pohlia wahlenbergii* 30. *Pohlia atropurpurea* (solid circles) and *Pohlia melanodon* (hollow circles). 31. *Pohlia brevinervis*. 32. *Pohlia vexans*. 33. *Pohlia columbica*.



MAPS 34–35. 34. *Pohlia longibracteata*. 35. *Pohlia integra*.

ACKNOWLEDGMENTS

H. Crum was a constant and invaluable source of inspiration and advice throughout this study. His time and interest is much appreciated. I am indebted to D. Vitt, who first suggested a study of *Pohlia*, and who guided me through early stages of the research. Curators too numerous to name made this revision possible by arranging loans of specimens. D. Ernet of the Landesmuseum Joanneum Graz, took considerable time to prepare labels and arrange a loan of type material for *P. proligera*. It was through my oversight that I neglected to thank him in a previous paper. This research was supported by grants from the Boreal Institute for Northern Studies, Edmonton, Alberta, with partial support from an NSF grant to William R. Buck and an NRC grant to D. Vitt.

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Contr. Univ. Mich. Herb. 15:297–309. 1982.

SELECTED SPECIES OF *LEUCOCOPRINUS* FROM THE SOUTHEASTERN UNITED STATES

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Herbarium and the Matthaei Botanical Gardens
The University of Michigan
and
Nancy S. Weber
Herbarium
The University of Michigan
Ann Arbor, Michigan 48109

The present contribution on *Leucocoprinus* is part of a larger project on the macrofungi of the southeastern United States by Nancy S. Weber, Alexander H. Smith, and Dan Guravich. Among the numerous problems encountered were collections belonging to the genus *Leucocoprinus*, some of which are here reported upon. This report covers those members of *Leucocoprinus sensu stricto* examined to date, but is not a comprehensive treatment of the genus for the Southeast.

The species discussed here are gilled mushrooms with thin-fleshed, typically fragile fruiting bodies whose buttons often resemble those of certain species of *Coprinus*. The pileus is striate to plicate-striate by maturity at least near the margin, and the lamellae are separated from the stipe by a collarium. The spores are smooth and white or nearly so in deposit. Brachybasidioles are present and usually inflated in the mature hymenium.

Dried material was studied in the usual manner for dried mushrooms. The pilear cuticle was studied using sections and squash mounts of the disc and about midway between the disc and the margin. Except as noted, all collections studied are deposited in the Herbarium of the University of Michigan (MICH). Color notations in quotation marks are taken from Ridgway (1912). Of particular importance to this project were the collections and excellent notes on them made by Ervin Hillhouse of Liverpool, Texas.

KEY TO SPECIES

1. Fruiting body white, dingy white, beige, tan, vinaceous, or lilac brown; lacking yellow colors. 2
1. Fruiting body yellow or yellowish, with or without a brown disc. 5
   2. Fruiting body white to dingy white, beige, or light tan; lamellae white or nearly so; spores hyaline to light ochraceous in KOH. 3
   2. Fruiting body vinaceous brown to lilac brown on the disc and scales of the pileus, similarly colored to paler elsewhere; lamellae and spores (in KOH) becoming pale peach color to pale flesh color at least in age. 1. *L. lilacinogranulosus*
3. Striae on pileus long, crowded, extending nearly to the disc; surface finely fibrillose to finely fibrillose-scaly. 2. *L. longistriatus*
3. Striae on pileus more widely spaced, shorter; surface covered with floccose scales or warts. 4
   4. Fruiting body pure white and remaining so (sometimes with a tinge of buff on the disc and surface of the stipe when bruised); soft warts present over the disc; typically fruiting singly or in small clusters. 3. *L. breviramus*
   4. Fruiting body off-white to dirty white, sometimes brownish or grayish; disc lacking warts, glabrous; typically fruiting in large clusters. 4. *L. cepaestipes*

5. Fruiting body exceedingly fragile; pileus membranous and soon collapsing. 6
5. Fruiting body ± fleshy and not collapsing when picked. 7
   6. Pileus bright yellow except for the brown disc; large cystidia (35–105 × 16–25 μm) present on young lamellae. 5. *L. magnicystidiosus*
   6. Pileus pale yellow, disc dull olive yellow; large cystidia absent from lamellae. 6. *L. fragilissimus*
7. Pileus pale greenish yellow with a contrasting brown disc; spores less than7 μm long. 7. *L. flavescens*
7. Pileus (including disc) bright or deep yellow; spores over 7 μm long. 8
   8. Pileus radially lacerate-fibrillose, scarcely striate until partially dried; spores lacking a conspicuous apical pore. 8. *L. flavus*
   8. Pileus at first covered with small floccose scales, distinctly striate when fresh; spores with a conspicuous apical pore. 9. *L. luteus*

1. **Leucocoprinus lilacinogranulosus** (Henn.) Locq., Bull. Soc. Linn. Lyon 12: 95. 1943.
Lepiota lilacino-granulosa Henn., Verh. Bot. Vereins Prov. Brandenburg 40: 145. 1889.

Illustrations: Pl. 1, Fig. 4, a–c; Pl. 2, Fig. 4, a, b.

Pileus 1.5–4.5 cm broad, 2.0–3.3 cm high at maturity, columnar and truncate at first, becoming broadly conic at maturity, plicate-striate nearly to the disc; cuticle over disc continuous, elsewhere breaking into fine scales which are more widely spaced toward the margin; buttons "deep brownish vinaceous" to "light grayish vinaceous," darkest over disc, mature specimens "benzo brown" over the disc and scales, otherwise "tilleul buff." Context thin. Odor and taste mild. Lamellae off-white to very pale pinkish buff in age, moderately crowded, becoming wrinkled in age. Stipe 4–5 cm long, 2.5–4.0 mm thick at the apex, 7.5–10.0 mm broad at the widest part of the somewhat bulbous base; white with a "light grayish vinaceous" cast over the base, unchanging when injured. Annulus thin, located just above the bulb. Spores 7.5–11.0 × 5.0–7.5 μm, elliptic to ovate in face view, inequilateral in profile, moderately to strongly dextrinoid, hyaline to pale peach color in KOH; apical pore prominent, with a hyaline, domelike cap. Basidia from young pileus 37–42 × 7.5–9.0 μm, 4–spored, apex truncate, base tapered. Brachybasidioles not readily demonstrated in young pilei where basidia are elongating, prominent in pilei with mature spores and then 12–16 μm in diam. Pleurocystidia not observed. Cheilocystidia 30–66 × 8–17 μm, clavate to irregularly elongate-inflated, hyaline, abundant on young specimens, apparently collapsed by maturity. Clamp connections not seen. Pilear cuticle over disc a zone several cells thick of inflated, mutually compressed, ± ellipsoid cells whose long axis is perpendicular to the surface of the cap; end cells staggered, not forming a palisade, contents pale rust color as viewed in KOH; toward the edge of the disc, cells become decumbent and longer; transition to radially-arranged hyphae evident, tips of hyphae in fascicles forming the scales. Cells in radially-arranged hyphae with peglike branches, slightly inflated, sometimes disarticulating under pressure, versiform cells increasingly abundant toward the margin and between scales, these cells often with stubby branches; cells in scales ellipsoid, subglobose, boomerang-shaped, or elongate-inflated, often with a dull purplish tan content.

Material studied. *Guravich 1280*, gregarious to cespitose in a longleaf pine nursery at the Harrison Experimental Forest of the De Soto National Forest, Harrison Co., MS; 10 July 1981. leg. Weber, Guravich, Cibula, and Izral.

This species was described from specimens that fruited in the orchid beds in the greenhouses of the Berlin Botanical Gardens, and so far as we know has not been previously reported from North America. Except that our specimens and

their spores are slightly larger than indicated for European material, they match the European description and illustrations well. Moser (1978) gives the spores as (7) 8.5–10.5 (12) × 6–6.5 (7.5) μm which approximates that observed in our material; however Hennings gave them as 10–13 × 7–9 μm and more recently Bon (1981) indicated they are 8–9.5 × 5.5–7 (8) μm. We are unable at present to account for these variations.

2. **Leucocoprinus longistriatus** (Peck) Smith & Weber, comb. nov.
Lepiota longistriata Peck, Bull. Torrey Bot. Club 25: 368. 1898.
Illustrations: Pl. 1, Fig. 2, a–c.

Pileus 4.3–8.0 cm broad, convex to plane or the margin uplifted in age, umbo distinct or not at maturity; surface plicate-striate nearly to the disc at maturity, striae fine, close, smooth; cuticle probably entire at first, remaining smooth over the disc but breaking up into fine fibrillose scales and fibrils especially over the ridges of the striae, scales easily brushed off; cuticle smoky brown to "vinaceous buff" over the disc, light buff becoming "ivory yellow" elsewhere. Lamellae "cartridge buff" to duller in age, edges very finely fimbriate, even, concolor. Stipe 4.0–8.3 cm long, 3–6 mm at the apex, 6–12 mm at the base when mature; shiny, glabrous, "cartridge buff" to "ivory yellow" or white, staining dull ochraceous when handled when young. Annulus a small, tight, ascending collar with a pale brown margin; usually located well below the midpoint of the stipe, often just above the small bulb, deciduous or persistent. Spores 6–8 (–9) × 4.5–5.0 μm, ovate in face view, elliptic in profile, lacking a distinct apical pore but under oil immersion there is a suggestion of a thin spot at the apex, not dextrinoid. Basidia 4–spored, 16–21 × 9–11 μm, scarcely projecting beyond the brachybasidioles. Pleurocystidia not seen. Cheilocystidia 21–33 × 8–12 μm, clavate or fusoid-ventricose, some mucronate or with a finger-like projection, hyaline. Pilear cuticle over the disc of radially arranged, anastomosing hyphae; the cells not inflated, many disarticulating at the septa and with a short branch just below the septum that forms a false clamp; cuticle over striate portion of fascicles of radially arranged hyphae 6–19 μm broad, end cells usually not erect, their apex rounded, slightly tapered, or clavate; content hyaline to light ochraceous brown in KOH. Clamp connections not seen.

Material studied. *Guravich 1349*, cespitose to scattered on chipped-bark mulch and on soil under sweet gum and live oak, Davis Bayou picnic area, Gulf Islands National Seashore, Ocean Springs, Jackson Co., Mississippi; 13 July 1981, leg. Weber and Guravich; *F. S. Earle*, Alabama, July (TYPE, NYS).

This species was described by Peck from specimens collected by F. S. Earle in Alabama and was later reported by Murrill (1911, 1972) from lawns and woods in Cuba and Jamaica as well as Florida. The distinguishing features are the numerous, fine, long striae on the cap, light bown disc and paler margin, and easily removed fibrils and scales.

Our notes on the microscopic features of the holotype follow: Spores 6.5–7.5 × 4.5–5.0 μm, ovate to elliptic in face view, elliptic in profile, lacking an obvious apical pore, faintly yellow as revived in KOH, not or only faintly dextrinoid. Basidia reviving poorly, about 10.5–13.5 μm broad, apparently embedded in a pavement of branchybasidioles, probably 4–spored as there are numerous tetrads of spores. Pleurocystidia not seen. Cheilocystidia 27–37 × 8–15 μm (length estimated only), subcylindric to clavate, abundant. Pilear cuticle over striate portion of ± radially arranged hyphae; the cells elongate, not inflated, seldom disarticulating, not distinctly pigmented; terminal cells rounded at the apex; hyphae seldom branched.

3. **Leucocoprinus breviramus** Smith & Weber, sp. nov.

Pileus 3.5–9.0 cm latus, conicus demum campanulatus vel late convexus, ad marginem brevistriatus vel non-striatus, candidus vel ad apicem sordide ochraceus, squamulosus demum glaber. Lamellae librae, albidae. Stipes 5.5–8.0 cm longus, 3–5 mm ad apicem, deorsum 10–12 mm crassus, annulatus, sursum glaber, albidus, tactu ± ochraceus. Annulus parvus, evanescens. Sporae 7.5–9.0 (10) × 5.5–6.5 μm, dextrinoideae, ad apicem pori praeditus. Pleurocystidia nulla. Cheilocystidia versiformia, 34–67 × 9–12 μm. Specimen typicum in Herb. Univ. Mich. conservatum est; legit E. *Hillhouse 264*, Liverpool, Brazoria Co., Texas, 6 Aug. 1971.

Illustrations: Pl. 1, Fig. 3, a, b; Pl. 2, Fig. 1, a, b.

Pileus 3.5–9.0 cm broad when fully mature, at first cylindric or finger-like, then conic to campanulate and finally plane or somewhat concave with the margin uplifted; striate near the margin only when mature, at times scarcely striate; snow white and remaining so except for a tinge of buff on the disc; covered with small rounded floccules which are smaller and denser on the disc, scattered toward the margin, easily rubbed off and sticking to the fingers; margin usually incurved until near maturity, frequently appendiculate with white floccules. Context white, 3–4 mm thick near the stipe, tapering and thin at the margin. Odor slightly musky, taste when raw mild. Lamellae white, unchanging, ventricose, of two lengths, about 15 per cm near the margin, edges even. Stipe 5.5–8.0 cm long, 3–5 mm thick at the apex, 10–12 mm thick at the elongate bulb; clothed with small floccules like those of the pileus below the annulus, glabrous above; white but at times staining slightly yellow when handled; hollow, stuffed, or solid. Annulus superior, rather small, membranous but mealy below, usually disappearing and leaving only small particles on the stipe, or remaining as a skirtlike ring, white. Spores 7.5–9.0 (10) × 5.5–6.5 μm, broadly ovate to elliptic in face view, elliptic in profile; the distinct small apical pore covered by a hyaline dome; dextrinoid. Basidia 4–spored, stubby. Brachybasidioles inflated. Pleurocystidia not seen. Cheilocystidia 34–67 × 9–12 μm; subcylindric to faintly ventricose or clavate; abundant; hyaline. Pilear cuticle over the disc of interwoven hyphae of variable diameter (3.5–12.0 μm broad), predominantly narrow at the surface, septate, not inflated, branched, the cells mostly irregular in shape, scattered, ± erect clavate cells present also especially in the scales; toward the margin of narrow hyphae that are tangled, not inflated and divided into short, branched cells suggestive of pieces of a 3-dimensional puzzle. Oleiferous hyphae present in context. Clamp connections not observed, but "false clamps" present.

Material studied. *Hillhouse 264* (TYPE, MICH), Liverpool, Brazoria Co., Texas, 6 Aug. 1971; also *Guravich 867*, Greenville, Washington Co., Mississippi, 29 Aug. 1977. Hillhouse reported that it usually fruits singly but sometimes in small clusters, on lawns, in gardens, and on wet hay in the summer and fall.

Dried fruiting bodies are warm ivory on the pileus, the lamellae are ± pinkish buff, and there are no signs of discoloration.

According to Hillhouse it is "some years plentiful and other years not to be found at all. Seems to be best during dry summers and comes on two or three days following a good shower. The summer of 1970 was a very wet year and I found none at all . . . the cespitose habit is not very prominent in this area with five in one tuft the most I have ever found; most are found as single. . . . Slight musky odor, raw taste mild, cooked taste of young buttons very good, no upsets from any amount eaten which at times have been large servings."

L. breviramus differs from *L. cepaestipes* by its persistent clean white appear-

ance, pileus that is striate only near the margin with prominent and persistent floccules on the disc, firm flesh, and non-cepsitose habit of fruiting. The specific epithet refers to the short, stubby branches of the cuticular cells.

L. breviramus is closely related to *Lepiota cretata* Locquin (in Haller, 1950) of Europe. However, Locquin proposed *Lepiota cretata* as a new name for *Agaricus cretaceus* Bulliard which is presumably the type for the species. An excellent description and discussion of *L. cretata* is presented by Josserand (1955). He described the species as a beautiful white *Lepiota* whose pilei are covered with snow white floccose scales as in the case with our species and he pointed out that his species could not be Buillard's species. In Builliard's illustration the covering of the pileus and stipe is clearly shown as consisting of slender fibrils intead of soft, almost globose to granular floccules. Josserand rejected the Builliard plate as representing Josserand's taxon as we reject it for ours. Consequently we also reject the name *Lepiota cretata* for our species.

Although there is considerable similarity between our species and that currently called *Leucocoprinus cretatus* in Europe, there are differences. The European taxon is seemingly more robust; fruits in large clusters; has larger spores, a bitter taste, and firm to hard flesh when young.

4. **Leucocoprinus cepaestipes** (Sow.: Fr.) Pat., Tab. Analyt. Fung. 7: 45. 1889.
Agaricus cepaestipes Sow.: Fr., Syst. Mycol. 1: 280. 1821.

Illustrations: Pl. 1, Fig. 1, a, b; Pl. 2, Fig. 3, a, b.

Pileus 2–8 cm broad, fragile, very thin, cylindric to ovoid, becoming broadly convex to plano-convex; white to whitish at first, becoming dingy white to buff and the disc often pale tan to yellowish brown; surface continuous over the disc and glabrous to minutely tomentose, toward margin decorated with fine mealy to fibrillose scales; disc truncate when young, sometimes umbonate at maturity; margin entire at first, becoming striate, striate-rimose, or plicate-striate to sulcate. Context thin, fragile, white or staining straw yellow to light pinkish cinnamon when bruised. Odor and taste not distinctive. Lamellae remote from stipe, crowded, thin, white becoming dingy white; margin even, finely fimbriate under a lens. Stipe 3–13 cm long, 2–6 mm at apex, enlarged downward and somewhat fusiform-ventricose to distinctly clavate toward the base, sometimes terminating in a short point in age; glabrous to faintly pruinose above, tomentose below; white at first, becoming delicately tinged pinkish tan to pale brown, sometimes straw yellow then light brown after handling. Annulus rather large, flaring, membranous with a lacerate margin, superior, white to whitish, subpersistent to evanescent. Spores 9–11 × 6.0–7.5 μm, ovate to subelliptic in face view, somewhat inequilateral in profile, obscurely truncate from a small apical pore, thick-walled, moderately to strongly dextrinoid, hyaline or in age dull ochraceous in KOH. Basidia 35–40 × 11–13 μm (estimated). Brachybasidioles present, reviving poorly. Pleurocystidia not seen. Cheilocystidia 37–66 × 7–16 μm (or longer, base hard to locate), clavate to bottle-shaped with a neck, sometimes forked at apex, hyaline, abundant on young lamellae, collapsing by maturity. Pilear cuticle over disc a zone several cells thick of inflated, versiform, globose, or ellipsoid cells 11–40 × 9–22 μm, these usually mutually compressed; giving rise to a turf of elongate erect or nearly so pileocystidia 45–99 × 4–9 μm; toward the margin of fascicles of radially arranged hyphae which give rise to sausage-shaped to oblong or irregular cells with stubby branches at the surface.

Material studied. *Hoseney 2115*, on lawn extension. 620 Church Street, Ann Arbor, Washtenaw Co., Michigan, 14 July 1972.

Observations. *L. cepaestipes* and its close relatives are considered "southern" species by most American mycologists and it is consequently included although

we have not found it there to date. It is, however, another common species which "everyone knows" but for which, when published descriptions are compared, there is no consensus on its characters. The concept presented here is adapted from H. V. Smith (1981) for the macroscopic characters and Hoseney 2115 for the microscopic features. This collection is the one illustrated in A. H. Smith and N. S. Weber (1980, pl. 163). In summary, although *L. cepaestipes* has been known to mycologists for about two centuries, the limits of the species are still in need of clarification.

5. **Leucocoprinus magnicystidiosus** Smith & Weber, sp. nov.

Pileus 4–8 cm latus, conicus, campanulatus vel planus, ad marginem valde striatus, laete luteus vel ad centrum brunneolus; fragilis; gustus leviter amarus. Lamellae luteae vel pallidior, 2–3 mm latae. Stipes 7–15 mm longus, 2–4 mm crassus, bulbosus, luteus, annulatus. Annulus superne albidus, inferus luteus, evanescens. Sporae 9.0–13.5 × 7.5–9.0 μm, valde dextrinoideae, ad apicem pori praeditus. Pleurocystidia 35–105 × 16–25 (30) μm, tenui-tunicata, ovoidea ellipsoidea vel subfusoidea. Cheilocystidia 18–25 × 10–17 μm, vesiculosa, clavata vel versiformia. Cuticula pileorum cellulae globosae vel subglobosae praeditus. Specimen typicum in Herb. Univ. Mich. conservatum est; legit *E. Hillhouse 266A*, Liverpool, Texas, Aug. 7, 1971.

Illustrations: Pl. 3, Fig. 1, a–g.

Pileus 4–8 cm broad when fully expanded, when young cylindric and up to 1.3 cm wide and 3.2 cm high, soon elliptic to narrowly conic becoming campanulate to plane or concave due to an uplifted margin; striate to plicate nearly to the disc; bright lemon yellow except for the brown disc when young, at maturity the striae bright yellow, grooves white; extremely fragile at all stages, sticking to the fingers and tearing readily; context white, less than 1 mm thick except at the disc. Odor not distinct, taste faintly bitter. Lamellae yellow to white, paler than the surface of the pileus, ventricose, 2–3 mm broad; lamellulae few. Stipe 7–15 cm long, 2–4 mm broad, equal or nearly so down to the somewhat bulbous base; yellow like the pileus or darker, sometimes reddish brown; extremely fragile, sometimes larger specimens break from their own weight. Annulus yellow below, white above; soon evanescent except for a flimsy ring on the stipe and a few small fragments appendiculate on the margin of the pileus. Spores 9.0–13.5 × 7.5–9.0 μm, ovate to ± lemon-shaped in face view, ovate to slightly inequilateral in profile, drawn out into a snout-like apex with a distinct pore covered with a domelike cap; moderately to strongly dextrinoid, the dome over the pore remaining hyaline; spore wall thick, complex. Basidia 4-spored, 20–39 × 10–12 μm, becoming greatly elongated at sporulation. Brachybasidioles inflated in mature specimens, 13.5–16.5 (–21) μm broad, forming a pavement. Pleurocystidia 35–105 × 16–25 (–30) μm, thin-walled, hyaline, elongate-elliptic tapering to a rounded or pointed apex, base narrow and pedicel-like; cystidia extend well beyond hymenium, often longer than lamellae are thick, most abundant near the edge of the lamellae, common in young specimens, presumably collapsed in old ones. Cheilocystidia of two types: 1) those similar in size and shape to the pleurocystidia, and 2) those 18–25 × 10–17 μm, abundant, variable in shape (vesiculose, broadly obovate, or pyriform), and persistent in old specimens. Pilear cuticle over disc a thick zone of inflated, mutually compressed cells terminating in a pavement of rounded cells 9–13 μm in diam; context below the cuticle of uninflated hyphae many with false clamp connection, numerous oleiferous hyphae also present; cuticle in striate portion a mixture of globose, subglobose, and inflated ellipsoid cells 15–72 × 13–54 μm, and narrow angular cells 3–8 μm broad with stubby branches.

Material studied. *Hillhouse 266A* (TYPE, MICH), 7 Aug. 1971, Liverpool, Brazoria Co., Texas; *A. H. Smith 14871,* 17 Aug. 1939, Cades Cove, Tennessee. Hillhouse gave the following information on 266A and two other collections not discussed here: "Summer and fall, scattered and gregarious on St. Augustine lawn and in pine and mixed woods growing from the soil and in layers of pine needles and leaves among grass, most abundant at times. Found only during and shortly after rains or in early morning when dews are heavy."

L. magnicystidosus differs from *L. fragilissimus* by its brighter colors and presence of immense pleurocystidia. *L. thoenii* Heinem. from Zaire is similar but has larger spores (11.4–16.0 × 8.4–10.0 μm) and lacks pleurocystidia.

L. magnicystidosus has extremely fragile fruting bodies, Hillhouse reported that the stipe was "extremely fragile and even a slight breeze will cause it to break once the fruit has reached maturity. I have had the stem break on specimens up to 8 cm across just from my breath while trying to get a picture. The larger specimens seem to sometimes break from their own weight. . . . Hot sun causes these to quickly deteriorate and disappear and none will be found except early in the morning on hot days." Dried specimens have a distinct vinaceous cast over the disc and the striae.

6. **Leucocoprinus fragilissimus** (Rav. in Berk. & Curt.) Pat., Essai Taxon. p. 171. 1900.

Hiatula fragilissima Rav. in Berk. & Curt. Ann. Mag. Nat. Hist., ser. 2, 12: 422. 1853.

Illustrations: Pl. 3, Fig. 1, a–c.

Pileus 2–5(–5) cm broad, becoming plane with a depressed umbo or the margin uplifted, striate nearly to the umbo, pulverulent with small yellow squamules except over the disc; disc "ecru olive" (dull olive yellow), to "deep colonial buff," elsewhere "pinard yellow" to "straw yellow;" fragile. Lamellae white, narrow, subdistant to crowded. Stipe 6–10 cm long, 1–2 mm thick at apex, 5–6 mm at base; fragile, pale yellow, powdery then glabrescent. Annulus small, superior. Spores 9–14 × 7.0–8.5 μm, broadly elliptic in face view, broadly inequilateral in profile; apex drawn out and almost snout-like, capped with a hyaline dome over the apical pore; apiculus inconspicuous; strongly dextrinoid. Basidia 21–25 × 9.0–10.5 μm, stout. Brachybasidioles 9–11 × 10–15 μm, abundant. Pleurocystidia not seen. Cheilocystidia 13–25 (–36) × 9–15 (–20) μm, broadly clavate, sometimes incrusted, single or in fascicles. Pilear cuticle over the disc a zone several cells thick of inflated, mutually compressed cells terminating in a pavement of rounded cells; transition to rest of pileus has mounds of inflated, more or less globose cells 12–54 × 12–41 μm in diam mixed with narrow (3.5–7.0 μm wide) hyphae whose cells are branched and irregular in shape, the whole apparently formed by the ends of radially aranged hyphae and continuing in this manner to the margin, a mixture of big cells and narrow ones, many of the inflated cells have diffuse smoky gray contents.

Material studied. *Guravich 1346*, scattered in mixed woods, Gulf Islands National Seashore, Ocean Springs, Jackson Co., Mississippi; 13 July 1981; leg. Weber and Guravich; also *Guravich 1268*, scattered under hardwoods, Harrison Experimental Forest of the De Soto National Forest, Harrison Co., Mississippi; 18 July 1981.

Sections mounted in KOH often release a yellow pigment; the disc and striae dry light gray to brownish gray. These fruiting bodies are almost unbelievably fragile and difficult to collect. *L. fragilissimus* was described from South Carolina and is widely distributed in tropical and subtropical regions: Pegler (1972) reported it from Ceylon (now Sri Lanka), and Heinemann (1977) reported it from Zaire.

7. **Leucocoprinus flavescens** (Morg.) H. V. Smith, Michigan Bot. 20: 50. 1981.
Lepiota flavescens Morgan, J. Mycol. 13: 5. 1907.

This species was described from southern Ohio and has been reported from greenhouses in Massachusetts and California as well. It fruits in warm humid habitats and we expect it will be found in the southeastern United States. The description is from H. V. Smith (1981).

Pileus (1.7–) 2.5–4.0 cm broad, cylindric-ovate becoming expanded to plane with an obtuse or flattened umbo, plicate-striate almost to the disc, pale greenish-yellow (near "napthalene yellow"), the disc brown and glabrous and contrasting strongly with the rest of the surface, ridges floccose to powdery, the grooves glabrous and white. Flesh thin, white. Lamellae yellowish, remote from the stipe, close to subdistant, narrow, subventricose. Stipe 3–6.5(–8) cm long, 2 mm thick at apex, enlarging to 3–5 mm thick at base, pale sulphur-yellow and covered wtih fine floccules like the pileus. Annulus superior, pale yellow, delicate and often evanescent. Spores 4.8–6.6(–7.2) × (3.5–)4.9–5.5 μm, broadly ellipsoid, subglobose or globose, pale yellowish-brown to rusty-brown in Melzer's sol., apical pore lacking. Basidia 15–18 × 7–8 μm, clavate. Brachybasidioles 14–18 × 10–15 μm, saccate and thin-walled. Cheilocystidia 17–43 × 8–15 μm, abundant, clavate, subcylindric, fusoid-ventricose with an obtuse apex, or cylindric with a short neck and a head. Lamellar trama loosely interwoven, oleiferous hyphae present. Pileal trama loosely interwoven, oleiferous hyphae present. Cuticle of pileus a compact layer of enlarged, clavate to pyriform, vesiculose, broadly fusoid-ventricose, or globose, thin-walled cells 10–50 μm broad which may also be found in clusters along the ridges of the striae, but generally not free-floating in the mount. Clamp connections not found.

8. **Leucocoprinus flavus** (Beeli) Heinem. Bull. Jard. Bot. Nat. Belg., Bull. Nat. Plant. Belg. 47: 84. 1977.
Lepiota flava Beeli, Bull. Soc. Roy. Bot. Belgique 64: 215. 1932.

Illustrations: Pl. 1, Fig. 1, a–c.

Pileus 1.8–2.7 cm broad, conic to broadly conic, radially lacerate-fibrillose, scarcely striate until dried, brilliant yellow with the umbo deeper in color and drying brown, umbo slight, disc lubricous. Context thin. Taste mild. Lamellae distant from the stipe. Stipe 5–6 cm long, about 2 mm at apex, nearly equal to a bulb 3–7 mm thick at the base, pale yellow, base sometimes with a small mycelial mass. Annulus flaring upward, membranous, persistent, pale yellow. Spores (6–) 7.5–9.0 × 3.8–5.3 μm, narrowly ovate to narrowly almond-shaped in face view, narrowly ovate to elliptic in profile; apical pore absent; wall not conspicuously thickened; spores moderately dextrinoid. Basidia 4–spored, approximately 25 × 9 μm, not reviving well. Brachybasidioles not conspicuously inflated at maturity. Pleurocystidia not seen. Cheilocystidia 33–49 × 7–11 μm, abundant, hyaline, subcylindric to somewhat fusoid-ventricose. Lamellar trama interwoven, of large cells. Minute refractive granules present in many cells in the hymenium. Pilear cuticle near the disc on mature pilei bearing mounds of short, curved (sausage-like) cells 4.4–10.5 μm broad, slightly inflated, sometimes bearing one or more branches, end cells broadly S-shaped or narrowly clavate; toward the margin of fascicles of radially arranged to loosely interwoven hyphae, hyphae unbranched, not disarticulating, 4.5–12.0 (–20) μm broad.

Material studied. *Weber 4583*, under mixed hardwoods, McCormick's Creek State Park, Owen Co., Indiana, 15 Aug. 1981.

Unlike most species in the genus, the margin of the cap in *L. flavus* does not become striate until the carpophore is at least partially dried. The brachy-

basidioles do not become inflated; Beeli (1932) described them as slenderly cylindric, and we had difficulty finding them. Our specimens agree well with the descriptions and illustrations given by Beeli (1932, 1936) and Heinemann (1977). This represents the first report of *L. flavus* from the United States. It seems likely that it will be found in the South as it was described from Zaire where warm, humid weather is also present.

9. **Leucocoprinus luteus** (Bolt.) Locq., Bull. Mens. Soc. Linn., Soc. Bot. Lyon 14: 93. 1945.
Agaricus luteus Bolton, An History of Fungusses growing about Halifax 2: 50. 1788.
Leucocoprinus birnbaumii (Corda) Sing., Sydowia 15: 67. 1962.
Agaricus birnbaumii Corda, Icon. Fung. 3: 48. 1839.

Illustrations: Pl. 1, Fig. 6, a, b; Pl. 2, Fig. 2, a, b.

Pileus 3.0–7.5 cm broad when mature; finger-like to conical at first, becoming broadly expanded to plane with a slight umbo; long striate to almost sulcate; covered with powdery to mealy, soft, floccose warts that are easily rubbed off; evenly lemon yellow to sulphur yellow. Context thin, at most 2–3 mm thick near the stipe, rather brittle when young, pliable when mature. Odor not distinctive; taste mild and pleasant but leaving a bitter aftertaste. Lamellae not crowded, pale yellow, soft and readily collapsing, of 3–4 lengths. Stipe 6–9 cm long, 3–4 mm thick at apex, up to 11 mm thick at the clavate base; minutely floccose-pulverulent near the base; brilliant yellow to pale greenish yellow; solid to pithy, usually hollow with age; white mycelioid covering sometimes present at the base. Annulus small, yellow, collar-like, often evanescent. Spores (8–) 9.0–10.5 (–12) × 6.0–7.5 μm, ovate in face view, inequilateral in profile; apex truncate or not, apical pore with a hyaline dome; wall thick; dextrinoid. Basidia 33–53 × 6–8 μm, elongate at the time of sporulation and projecting well beyond the surrounding brachybasidioles. Brachybasidioles broad, inflated to subglobose, some with weakly dextrinoid content. Pleurocystidia not seen. Cheilocystidia 40–66 × 10–15 μm; clavate, elongate, tapered, ± ventricose, or irregular, some with finger-like apical projection; abndant; hyaline; collapsing at maturity. Pilear cuticle over the disc of hyphae with a mixture of short, branched, uninflated cells and predominantly of inflated, sausage-shaped, ellipsoid, pyriform to subglobose or globose cells; toward the margin of loosely interwoven hyphae forming mounds of narrow intact hyphae and short, disarticulated cells with stubby branches.

Material studied. *Hillhouse 147*, Liverpool, Brazoria, Co., Texas; 13 June 1970; *Guravich 1373*, Davis Bayou picnic area, Gulf Islands National Seashore, Ocean Springs, Jackson Co., Mississippi; 17 July 1981, leg. Weber and Guravich. Hillhouse reports that this species occurs on decaying plant material, particularly decaying hay, in rich garden soil, on lawns or rarely on logs or stumps or in shaded lawns under live oak from late spring to fall in Texas.

This species is often found in greenhouses and similar environments such as shopping malls in cooler regions but it grows outdoors in the warm regions of the world. It has been reported to be poisonous, but Hillhouse recorded the following observations on collection 147: "Cooked taste about like the commercial variety of *Agaricus* but with a slight bitter aftertaste. I have eaten fairly large amounts of these on several occasions without upset of any kind. For the past three or four years I have had about a hundred bales of hay stacked near my garden where I use it for mulch. I have had large amounts of this mushroom and another I believe to be *Lepiota cepaestipes* come up in the hay and in my garden. I eat both without upset."

The use of the pre-Freisian epithet *luteus* instead of the post-Friesian epithet *birnbaumii* is mandated by the rule changes promulgated at the International Botanical Congress in Sidney, Australia in 1981.

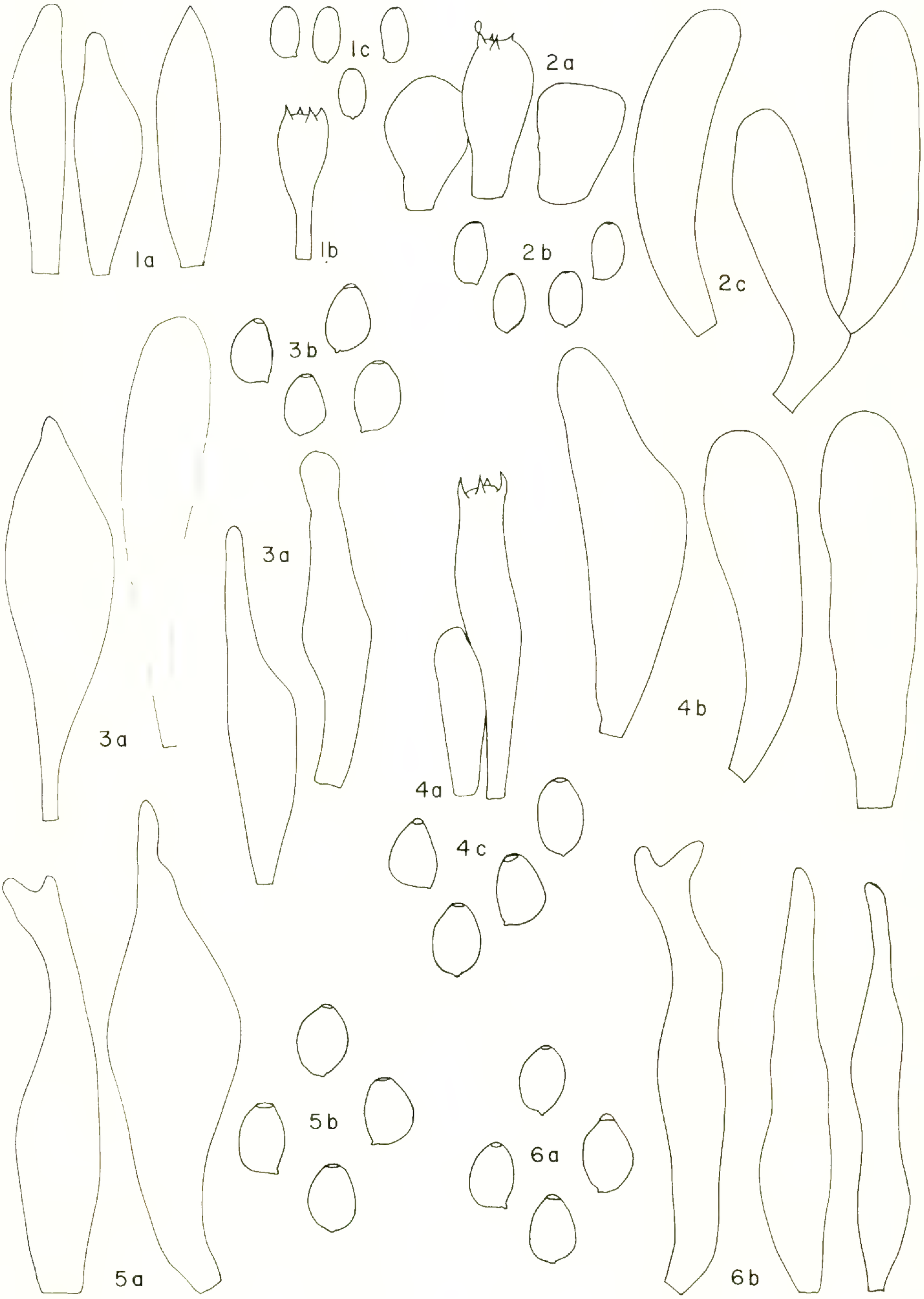

PLATE 1. FIG. 1, *L. flavus* (*Weber 4583*), a, cheilocystidia; b, basidium; c, spores. FIG. 2, *L. longistriatus* (*Guravich 1349*), a, basidium and brachybasidioles; b, spores; c, cheilocystidia. FIG. 3, *L. breviramus* (*Hillhouse 264*), a, cheilocystidia; b, spores. FIG. 4, *L. lilacinogranulosus* (*Guravich 1280*), a, basidium and brachybasidiole; b, cheilocystidia; c, spores. FIG. 5, *L. cepaestipes* (*Hoseney 2115*), a, cheilocystidia, b, spores. FIG. 6, *L. birnbaumii* (*Hillhouse 147*), a, spores; b, cheilocystidia. All ×1,000.

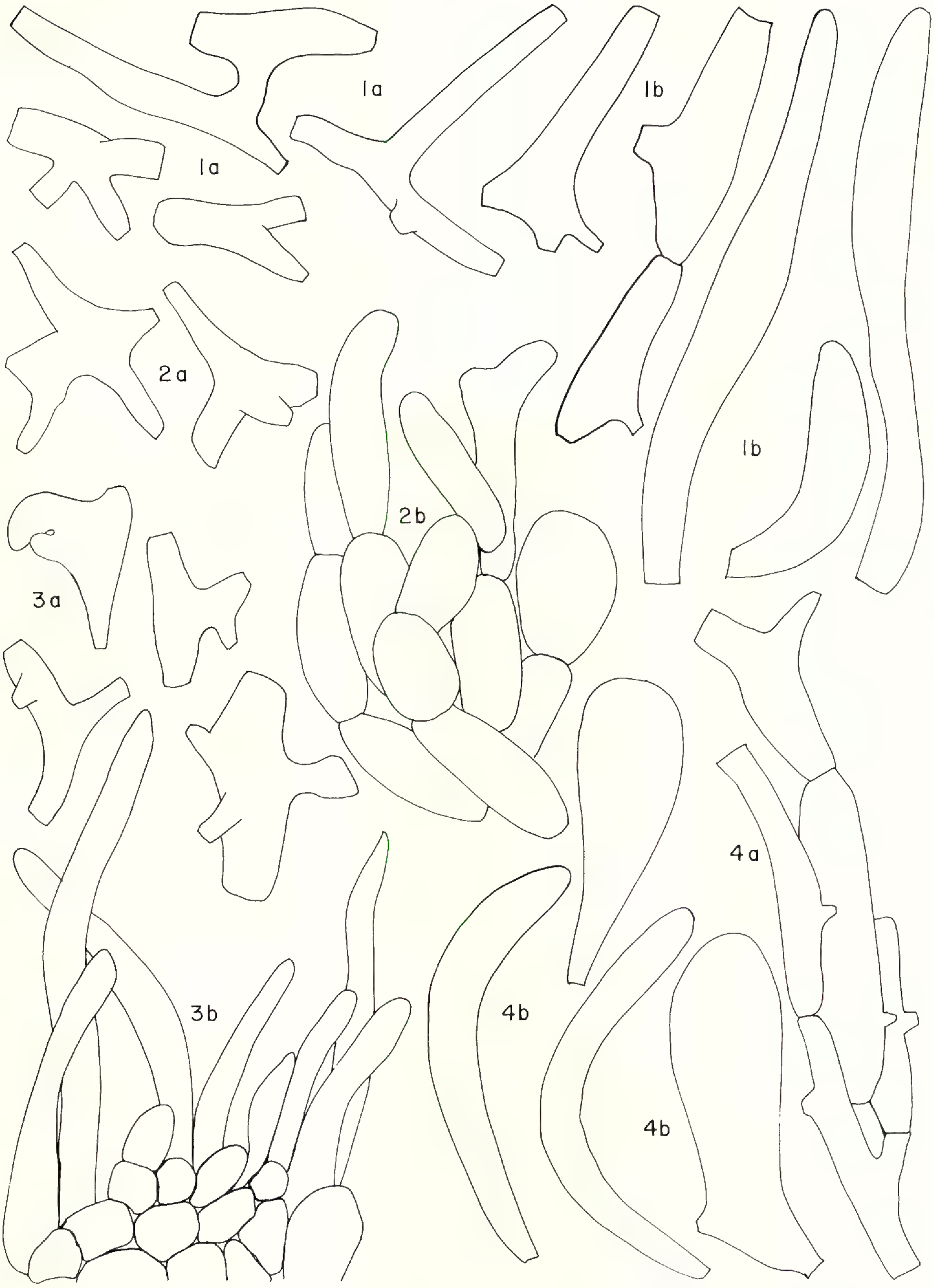

PLATE 2. FIG. 1, *L. breviramus* (*Hillhouse 264*), a, cells from plicate portion; b, cells from disc. FIG. 2, *L. birnbaumii* (*Hillhouse 147*), a, cells from plicate portion; b, cells over disc. FIG. 3, *L. cepaestipes* (*Hoseney 2115*), a, cells from plicate portion; b, section of cuticle over disc. FIG. 4, *L. lilacinogranulosus* (*Guravich 1280*), a, hyphae over plicate portion; b, cells from disc. Fig. 1 ×1,000, all others ×800.

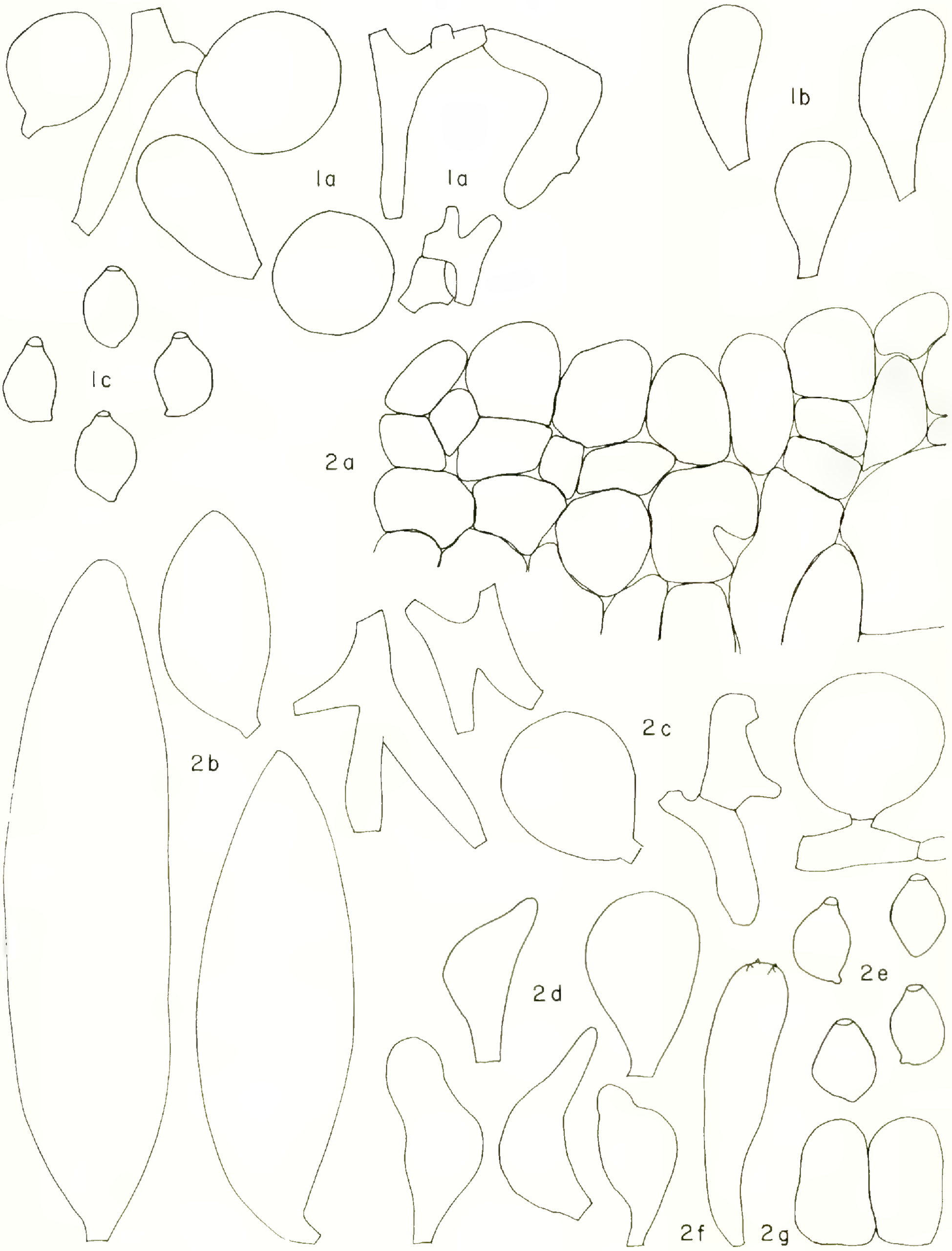

PLATE 3. FIG. 1, *L. fragilissimus* (*Guravich 1346*), a, cells from striate portion of pileus; b, cheilocystidia; c, spores. All ×800. FIG. 2, *L. magnicystidiosus* (*Hillhouse 266A*), a, section of pilear cuticle over disc; b, large cystidia, both pleuro- and cheilocystidia; c, cells from cuticle in striate portion; d, persistent cheilocystidia; e, spores; f, basidium; g, brachybasidioles. All ×1,000 except a & c which are ×800.

ACKNOWLEDGMENTS

The directors and staff of the Matthaei Botanical Gardens and the Herbarium generously allowed us to use their respective facilities. Alexander H. Smith provided many pertinent suggestions and the Latin diagnoses. The junior author's field work was aided by Dr. Harold Howse who made the facilities of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi available. Dr. William Cibula helped her become acquainted with Mississippi and its mushrooms. The courtesy and cooperation of the staffs of the Harrison Experimental Forest of the DeSoto National Forest and the Gulf Islands National Seashore in allowing her to collect in their respective areas is much appreciated.

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Contr. Univ. Mich. Herb. 15:311–313. 1982.

A NEW SPECIES OF *RHYNCHOSPORA* (CYPERACEAE) FROM VENEZUELA

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According to Koyama's treatment of the Rhynchosporeae for the Botany of the Guyana Highland (1972), over 86 species of *Rhynchospora* are known from Venezuela. Despite Koyama's important contribution to our knowledge of Venezuelan *Rhynchospora* there still exist species to be described.

Because of its capitate inflorescence, white spikelet scales, and lack of hypogynous bristles, *Rhynchospora chimantensis* at first appears to be a new species of section *Dichromena*. However, it has several features uncharacteristic of section *Dichromena* which are found in section *Pseudocapitatae* (Kükenthal, 1949): achenes 1–2 per spikelet, basal spikelet scales smaller than those more distal, relatively loosely aggregated spikelets in fascicles, and achene surfaces which are only lightly rugulose. For these reasons, I did not include this species in my recent revision of *Rhynchospora* section *Dichromena* (Thomas, 1982) but consider it allied to section *Pseudocapitatae*.

Rhynchospora chimantensis Thomas, sp. nov. Fig. 1.

Cespitose perennial; culms erect to arching, to 60 cm tall, 1.1–1.3 mm wide basally, 0.8–0.9 mm wide distally, obtusely triquetrous, glabrous, green; leaves 3–5, 1–2 cauline, green to greyish-green; leaf blades 5–30 cm long, 1.5–3 mm wide, flat to conduplicate, lateral veins ± prominent, sparsely villous or glabrous adaxially except for the villous midrib, villous abaxially; margins villous; leaf sheath 3–5 cm long, villous; inner band whitish, chartaceous, densely short-villous, its summit truncate to concave; inflorescence bracts 1–3, green to greyish-green, flat to conduplicate, midrib prominent, base whitish; basal bract longest, 4.2–6 cm long, 1.6–1.9 mm wide, linear, white along basal 3.5–6 mm and an extension along midrib, sparsely pilose, more densely so along adaxial midrib; inflorescence congested, globose, head-like, with 24–38 fascicled spikelets with basal peduncles occasionally to 3 mm long; spiklets ovoid to lanceoloid, 4–7 mm long, 0.8–1.3 mm wide, with ca. 9–10 scales; scales ovate, ca. 5 mm long, ca. 1.8 mm wide, smaller towards base of spikelet, cymbiform, distal ⅓ carinate, white to pinkish, lightly and finely streaked with reddish brown basally; stamens 3; filaments 2.9–3.3 mm long; anthers 2–2.1 mm long; stigma and style 3.1–3.6 mm long; stigma branches 2.3–2.6 mm long; achene lenticular, usually bilaterally symmetrical, ellipsoid, yellowish or beige darkening to light reddish-brown at base, 1.1–1.3 mm long, 0.7–0.9 mm wide; edges of style base confluent with margins of achene; style base persistent, triangular, 0.6–1 mm long, 0.6–0.7 mm wide, brown; summit of achene horizontal; achene surface transversely rugulose, often indistinctly so; epidermal cells narrowly elliptic, often indistinct.

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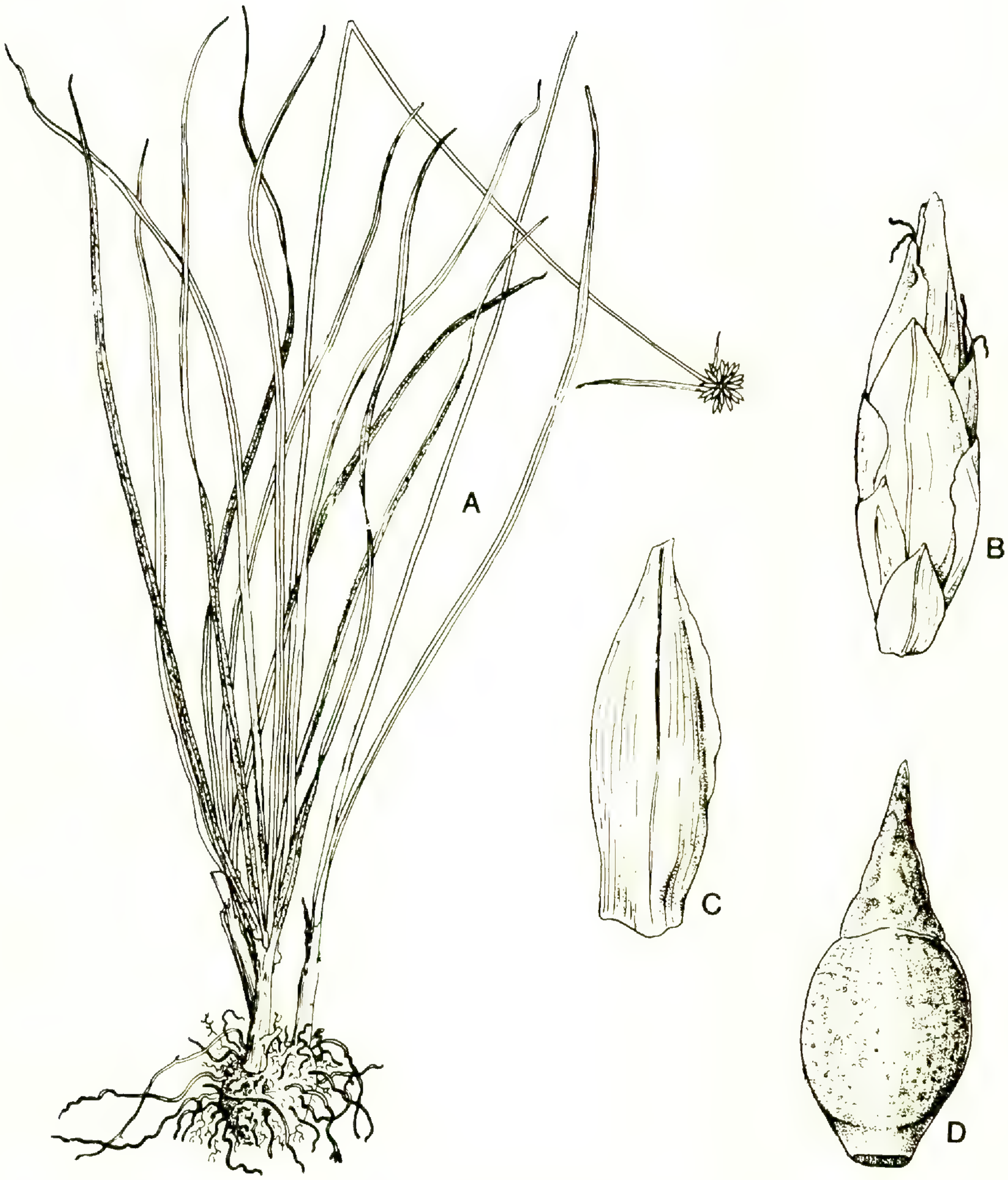

FIG. 1. *Rhynchospora chimantensis*. A. Whole plant, culm 60 cm tall; B. Spikelet, 5 mm long; C. Spikelet scale, 4 mm long; D. Achene, 1.8 mm long (*Steyermark & Wurdack 362* (NY)).

Planta caespitosa, perennis; culmi erectiusculi vel arcuati, usque ad 60 cm alti; foliorum laminae 5–30 cm longae, adaxialiter glabrae vel villosae, abaxialiter villosae; laminarum costae villosae; inflorescentia laxe congesta, globosa; spiculae 24–38, ovate vel lanceolate, 4–7 mm longae, 0.8–1.3 mm latae, 1–2 achaeniis; achaenium lenticulare, ellipsoideum, 1.1–1.3 mm longum, 0.7–0.9 mm latum; achaenii testa leviter transverse rugulosa.

VENEZUELA: BOLIVAR: Chimantá Massif, Central Section, scrub forest near Summit Camp, rare on dry sandy banks bordering river, heads gray-white, 1925 m, 2 Feb. 1955, *Steyermark & Wurdack 362* (F, holotype; MO, NY isotypes).

Although this species is known from only one collection, it is quite possible that it occurs on other tepui mountains as well as on Chimantá. *R. chimantensis* is characterized by its height, narrow leaves, green bracts with pilose midribs, the loosely congested head of spikelets, the ellipsoid achenes, and the long style

bases. Despite having seen only one collection (3 sheets), I feel that there is little possibility of this being simply an extreme variant of a previously described taxon.

ACKNOWLEDGMENTS

I would like to thank the curators of F, MO, and NY for the loan of their specimens and Ms. Kathy Simpson for the line drawing she prepared.

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BOTRYCHIUM RUGULOSUM (OPHIOGLOSSACEAE), A NEWLY RECOGNIZED SPECIES OF EVERGREEN GRAPEFERN IN THE GREAT LAKES AREA OF NORTH AMERICA

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The name *Botrychium ternatum* (Thunb.) Sw. was long applied to the evergreen grapeferns (*Botrychium* subg. *Sceptridium*) of North America. Not until Underwood's pioneering revision of 1898 did there arise any question as to whether true *B. ternatum*, an Asiatic species described originally in 1784 from Nagasaki, Japan, really occurred in North America at all. In his opinion, nothing known to him from the New World could be identified as *B. ternatum*. However, in the late 1950's, Wagner (1959) encountered grapeferns in Michigan that seemed at the time to be the same as, or closely related to, the Japanese species, and its name was once again taken up for certain American collections by various authors. Wherry (1961) referred to the plants in question as the "American ternate grapefern" and described it as "a relative of the Asiatic taxon." Other authors, including ourselves, subsequently simply referred to it as *B. ternatum* without qualification.

In connection with monographic research on *Botrychium* during the past several years, it has become evident that typical *B. ternatum* does not occur in North America, and that the plants that we referred to are distinct from that species in a number of characters. They constitute a new species, closely related to two much more common species that usually occur with it, the endemic American *B. dissectum* Spreng. and the circumboreal *B. multifidum* (Gmel.) Rupr. The purpose of this paper is to describe this new species and to compare it with species of near relationship.

Botrychium rugulosum W. H. Wagner, sp. nov.

Frons deltoidea, 3 (–4)-pinnata, pinnis usque ad apicem divisis, pinnulis ultimis angulatis, oblique rhomboideis, lanceolatis vel oblongis, 0.2–0.5 cm latis, vivis convexis et rugulosis, marginibus grosse dentatis (raro subintegris).

In habit resembling *B. dissectum* and *B. multifidum* with which it usually grows, its fronds emerging from the ground before the former and after the latter. Sterile blades deltoid (Fig. 1, 2) the stalk more or less the same length as the blade (shorter in sun forms, longer in shade forms), the stalk and blade together of mature, fertile plants averaging 8–16 cm (3 cm in sun to 30 in shade), the blade itself averaging 4–8 (2–16) cm long. Sterile blade 3–(2–4)-pinnate, divided to the pinna tips with regular reduction in symmetry. Lateral and basal pinnae ovate-deltoid, the pinnules rhomboidal, ovate, or oblong, usually strongly angled, 0.2–0.5 cm wide, the laminar surface in the living state convex above and more or less coarsely rugulose (Fig. 1, Wagner 1962, Pl. 1). Pinnule margins with nearly regular, somewhat rounded, wide teeth (except in rare

FIG. 1. Frond of *Botrychium rugulosum* (Michigan: Gratiot Co., w. of Meridian Rd., Fall, 1981). Note rugulose and convex segments, indicated by arrow.

subentire forms) (Fig. 2). Lateral veins mainly somewhat spreading rather than nearly parallel (Fig. 3). Chromosomes $n = 45$.

TYPE: U.S.A., MICHIGAN, Midland Co., Mills Twp., south side of Baker Road, sect. 29, R. 2E, T. 16N. Common in more or less open, dry, sandy field with scattered trees and shrubs, east of oil well. 9 September 1959. *W. H. Wagner 9099, M. Sargent, and R. L. McAdams.* (MICH).

Botrychium multifidum (Gmel.) Rupr. f. *dentatum* R. Tryon (1939) is a synonym, based upon compact forms of *B. rugulosum* from northern Wisconsin.

COLLECTIONS EXAMINED

CANADA: ONTARIO: CARLETON CO.: Merivale, *Minshall s.n.*, no date (DAO). MIDDLESEX CO.: Near London, *Balkwill, J.A. s.n.*, 10 Oct 1893 (MICH.) MUSKOKA CO.: Georgian Bay I, Beausoleil I, *Stirrett 1212*, no date (DAO). NORTHUMBERLAND CO.: Castleton, *Macoun, J. s.n.*, Aug 1860 (NY). COUNTY UNKNOWN: Lake region and Ontario, *Macoun, J. s.n.*, 15 Aug 1874 (MTMG).

QUEBEC: CHAMBLY CO.: Chambly, *no collector*, 25 Sep 1927 (MTMG). GATINEAU CO.: Ironside, Hull, *Rolland-Germain 97*, no date (MTMG). RICHELIEU CO.: St-Joseph-de-Sorel, *Marie-Victorin, F 28082*, 23 Sep 1928 (GH). STANSTEAD CO.: Hatley, *Mousley, H. s.n.*, 1919 (US). TERREBONNE CO.: Terrebonne, *Terrill s.n.*, 23 Oct 1927 (MTMG). VAUDREIL CO.: Rigaud, *Robert, C.S.U. s.n.*, no date (DAO).

UNITED STATES: CONNECTICUT: WINDHAM CO.: Brooklyn, *Merritt, A.O. s.n.*, Oct 1903 (MICH).

MICHIGAN: BENZIE CO.: Sect 1, NW Shorter Lake, *Hagenah, D.J. 6585*, 12 May 1967 (BLH). CHIPPEWA CO.: Sugar I, Sect 33, *Hiltunen, J.K. 2695*, 4 Sep 1960 (MICH.) CLARE CO.: Sect 16, 17, S side Rte 115, *Wagner, W.H. et al. 63193*, 14 Nov 1963 (MICH). GRAND TRAVERSE CO.: Sand Lake, *Wagner, W.H. et al. 9389*, 22 May 1961 (US). SE Traverse City, Sect 28, *Wagner, W.H. & F.S. 9451*, 5 Jul 1961 (MICH). SE Traverse City, unnamed lake, *Wagner, W.H. et al. 9316, 9319, 9322*, 1 Oct 1960 (all MICH). Sect 29, T 27 N, R 9 W, *Hagenah, D.J. 4516*, 1 Oct 1960, *4614*, 3 Jun 1961 (both BLH). 11 mi ESE Traverse City, beach small lake, *Dieterle, J.V. 1981*, 4 Sep 1960 (MICH). GRATIOT CO.: Sect 25, ½ mi S M-46, W of Meridian Rd, *Wagner, W.H. & F.S. 9442*, 2 Jul 1961, *Wagner, W.H. et al. 8679* 12 Apr 1959, *9108*, 20 Sep 1959 (all MICH). IOSCO CO.: Sect 5, T 23

FIG. 2. Sterile frond silhouettes of eastern North American *Botrychium* subg. *Sceptridium* (all MICH). R = *B. rugulosum* (Michigan): (1) Monroe Co., *8670*, (2) St. Clair Co., *Hagenah H-S-T*, (3) Monroe Co., *8594*, (4) Monroe Co., *8598*, (5) Coarse form, Monroe Co., *8594*, (6) Saginaw Co., *70503*; (7) Juvenile form, Monroe Co., *8598*, (8) finely cut form, Muskegon Co., *Voss 9180*. M = *B. multifidum* (Michigan): (1) Keweenaw Co., *McVaugh 11146*, (2) Wexford Co., *9314*. D = *B. dissectum* (Indiana): (1) Jefferson Co., *D. M. Smith SDM-5-1*, (2) the same, *SDM-2C-1*, (3) Dissected extreme, the same, *SDM-3A-B*. (All field nos. without collector designated are W. Wagner).

N, R 5 E, *Wagner, WH. et al. 9329*, 2 Oct 1960 (MICH). JACKSON CO.: ½ mi ENE Trist & Seymour Rds, *Wagner, W.H. 73460*, 13 Oct 1973 (MICH). KALKASKA CO.: Sect 14, 4 mi W Kalkaska, *Hagenah, D.J. 4606*, 3 Jun 1961 (BLH). KENT CO.: Lake Shore Dr 1 mi S Kent City, *Wagner, W.H. et al. 9205a*, 23 Apr 1960 (BLH, MICH). LEELANAU CO.: NW Cook Lake, Sect 35, *Hagenah, D.J. 6582*, 12 May 1967 (BLH). LIVINGSTON CO.: Near Lime Lake, *Wagner, W.H. et al. 62358*, 26 Oct 1962 (MICH). S side Sayle's Lake, *Wagner, W.H. 8417*, 27 Jun 1957 (MICH). MIDLAND CO.: E side Jefferson Rd near Shearer, *Wagner, W.H. & Blasdell, R.F. 8999*, 3 Jun 1959 (MICH). Sect 29, NW ¼, E of oil well, *Wagner, W.H. et al. 9029*, 11 Jun 1959, *9099*, 9 Sep 1959,*9258*, 14 Jul 1960 (all MICH).

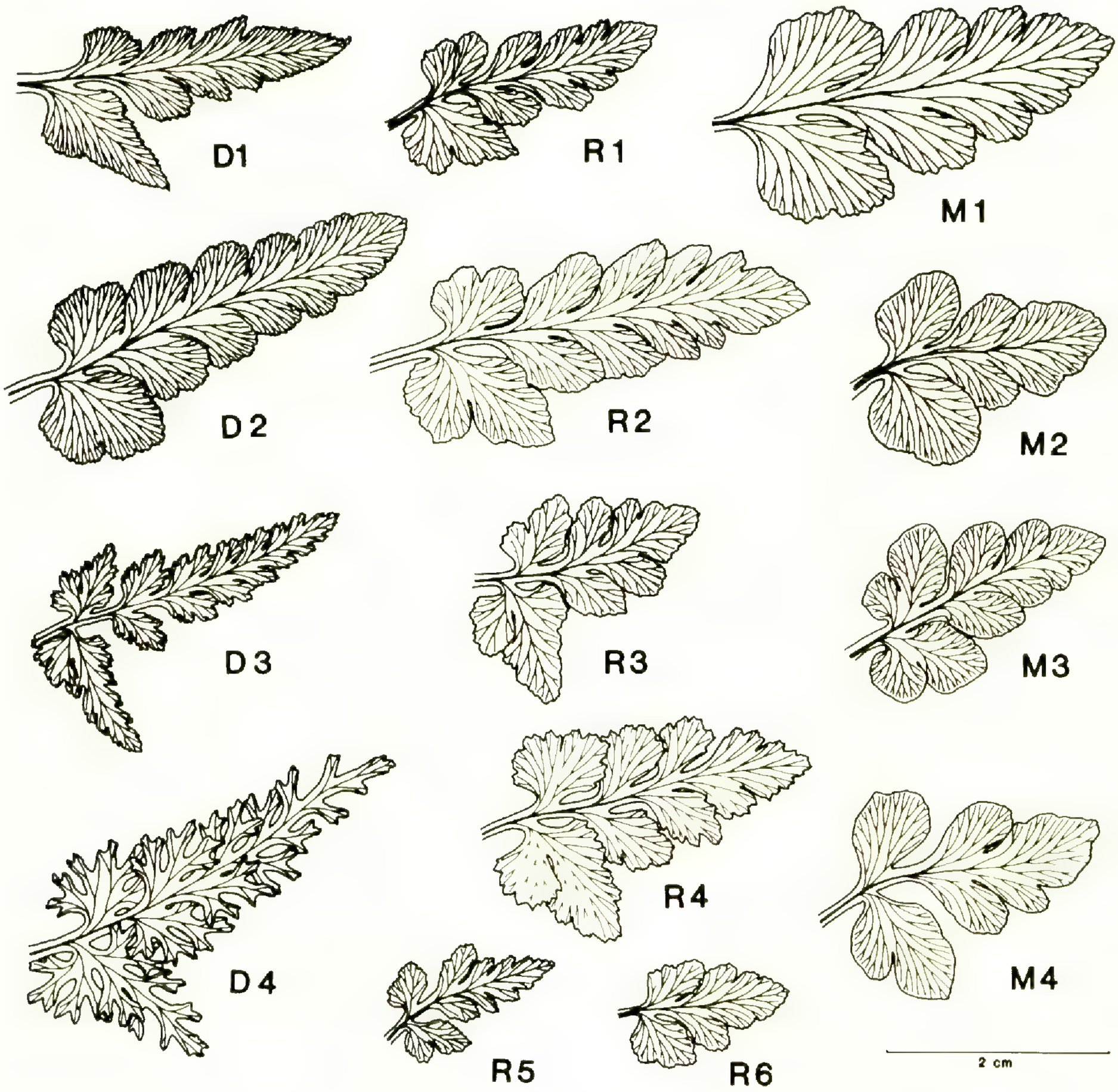

FIG. 3. Segment shapes and venation patterns of eastern North American *Botrychium* subg. *Sceptridium* (all MICH). R = *B. rugulosum* (Michigan): (1) Monroe Co., *8603*, (2) Monroe Co., *9123*, (3) Gratiot Co., *9108*, (4) Midland Co., *9099*, (5) same as (1), (6) same as (4). M = *B. multifidum* (Michigan): (1) Midland Co., *9097*, (2) same as (1), (3) Mecosta Co., *9116*, (4) St. Clair Co., *9053*. D = *B. dissectum*: (Michigan): (1) Monroe Co., *8596a*, (2) Cheboygan Co., *8063a*, (3) Midland Co., *9096*, (4) (Canada, Ontario): Kent Co., *9158*. (All field nos. are W. Wagner.)

W side Sect 15, Kawkawlin R, *Hagenah, D.J. 4623*, 10 Jun 1961 (BLH). MISSAUKEE CO.: Sect 22, T 23 N, R 7 W, *Hagenah, D.J. 5027*, 11 Aug 1962 (BLH). MONROE CO.: Dixon Rd, 2 mi NE Petersburg, *Wagner, W.H. 8396b*, 11 Jun 1957, *9067*, 12 Jul 1959, Wagner, W.H. & BLASDELL, R. F. *8594*, 16 Sep 1958 (all MICH). Grames Rd near Tuttle Hill Rd, *Wagner, W.H. 8598*, 16 Sep 1958, *Wagner, W.H. & McAdams 9126*, 9 Oct 1959 (both MICH). Ida Twp, *Wagner, W.H. & Hauke, R. & K. 8632*, 2 Oct 1958, *Wagner, W.H. & McAdams 9123*, 9 Oct 1959 (both MICH). Ida Twp, E of US-23 near irrigation ditch, *Wagner, W.H. 8670*, 14 Nov 1958, *Wagner, W.H. & Blasdell, R.F. 8649*, 18 Oct 1958, *Wagner, W.H. & Hagenah, D.J. 8635*, 4 Oct 1958, *Wagner, W.H. & McAdams 9123*, 9 Oct 1959, *Wagner, W.H. et al. 8670*, 14 Nov 1958, *9261*, 4 Aug 1960, *s.n.*, 2 Nov 1961 (all MICH). Plank Rd near Ostrander Rd, *Wagner, W.H. & White, R.A. 9100–3*, 16 Sep 1959 (MICH). Rutherford's, Dixon Rd, *Wagner, W.H. & Blasdell, R.F. 8594*, 16 Sep 1958, *Wagner, W.H. & Sargent, M 9066*, 5 Jul 1959 (both MICH). Sect 5, Hitchingham Rd, *Blasdell, R.F. 300*, 12 Oct 1958 (MICH). W of Plank Rd, N of Ostrander Rd, *Wagner, W.H. & Shetler, S. 8603*, 19 Sep 1958 (MICH). MONTCALM CO.: E of 131, S of Mecosta Co, *Wagner, W.H. et al. 9114*, 26 Sep 1959 (MICH). MUSKEGON CO.: Gerber Scout Reservation, *Wagner, W.H. 9249*, 5 Jul 1960 (MICH). NW of Holton, *Voss, E.G. 9180*, 13 Sep 1959 (MICH). OGEMAW CO.: Sect 29, T 23 N, R 3 E, *Wagner, W.H. et al. 9326*, 2 Oct 1960 (MICH). OSCODA CO.: Wagner Lake, *Wagner, W.H. 70163*, 30 Apr 1970 (MICH). Wagner Lake, Sect 13, *Hagenah, D.J. 6039*, 21 Apr 1963 (BLH). SAGINAW CO.: Fordney Rd, *Wagner, W.H. et al. 9048*, 21 Jun 1959 (MICH). Fordney Rd, N of Brady Rd, *Wagner, W.H. et al. 8589*, 15 Sep 1958, *9045–5*, 21 Jun 1959 (both MICH). SAGINAW CO.: M-46, S of Hess Rd, *Wagner, W.H. 70503*, 4 Nov 1970 (MICH). Nehmer's Woods, W of Saginaw, *Case, F. s.n.*, 25 Sep 1958 (MICH). Rte 85, 5 mi S

Frankenmuth, *Churchill, J.A. s.n.*, 20 Aug 1956 (MSC). 1⅓ mi E Burt, *Wagner, W.H. et al. 8586*, 15 Sep 1958 (MICH). 1/5 mi S Gratiot Co line, *Wagner, W.H. et al. 8683*, 12 Apr 1959 (MICH). 2¾ mi N Chapin, *Wagner, W.H. et al. 9104*, 20 Sep 1959 (MICH). 6/10 mi N Birch Run Rd, *Wagner, W.H. 8520*, 22 Mar 1958 (MICH). ST CLAIR CO.: Algonac, *Farwell, O.A. 3552–5*, 12 Oct 1913, *7260*, 15 Oct 1924 (both BLH). E side Wales Rd, *Wagner, W.H. et al. 9305*, 23 Aug 1960 (MICH). N side Nolan Rd, *Wagner, W.H. et al. 62010*, 31 Mar 1962 (MICH). N side Rte 21, *Wagner, W.H. 9055*, 26 Jun 1959, *9311*, 23 Aug 1960 (MICH). NE edge Algonac, *Wagner, W.H. et al. 9163*, 20 Dec 1959 (MICH). Nolan Rd, Hagenah, D.J. H-S-T, 11 Nov 1961 (MICH). TUSCOLA CO.: Swaffer & Bray Rds, *Wagner, W.H. & Barnes 8616*, 23 Sep 1958 (MICH). WASHTENAW CO.: Waterloo Rec Area, N of Cedar Lake, *Wagner, F.S. 81026*, 12 May 1981 (MICH). 1 mi NE Willis McKean Rd, *Grether, D.F. s.n.*, 6 May 1956 (MICH). WAYNE CO.: Center Sect 30, Sumpter Twp, *Wagner, W.H. & Blasdell, R.F. 8614*, 22 Sep 1958, *Wagner, W.H. et al. 9194a, 9194b*, 30 Mar 1960 (all MICH). Huron R Dr, junct Flat Rock, I-94, *Wagner, W.H. & Morzenti 9220*, 20 May 1960, *Wagner, W.H. et al. 8640–5*, 11 Oct 1958 (both MICH). Merriman Rd, near Pennsylvania Rd, *Wagner, W.H. 9347*, 12 Mar 1961 (MICH). N side Oakville-Wally Rd, *Wagner, W.H. 62095*, Jun 1962 (MICH). Sect 11, off Willis Rd, *Blasdell, R.F. 299*, 3 Oct 1958 (MICH).

MINNESOTA: AITKIN CO.: N side Rte 200, 5 mi E Cass Co, *Wagner, W.H. & F.S. 79316–1*, 28 Jul 1978 (MICH).

NEW YORK: HERKIMER CO.: Dutch Hill, 6 mi E Utica, *Haberer, J.V. 1901*, Nov 1905 (US). MADISON CO.: Lenox, Oneida Lake, *Haberer, J.V. s.n.*, Oct 1906 (US). ST LAWRENCE CO.: Parishville, *St John, E.P. s.n.*, 11,21 Sep 1942 (US). 3 mi SW Parishville, *St John, E.P. s.n.*, 28 Jul 1943 (US). 3 mi W Parishville, *St John, E.P. s.n.*, 2 Aug 1943 (MICH).

VERMONT: ADDISON CO.: Base Green Mt, Middlebury, *Brainerd, E s.n.*, 8 Sep 1899 (NY). Bristol, *Hosford, F.H. s.n.*, 26 Sep 1878, *Pringle, C.G. s.n.*, 26 Sep 1878 (both NY). Bristol, Cobble Hill, *Brainerd, E s.n.*, 12 Sep 1900 (MO). Mt Philo, *Wagner, W.H. & Lellinger, D.B. 9084*, 19 Aug 1959 (MICH). CALEDONIA CO.: St Johnsbury, Harris Hill, *Rooney, B.M. s.n.*, 22 Oct 1903 (US). St Johnsbury, Padduck Village Cemetery, *Rooney, B.M. s.n.*, 9 Oct 1902 (US). CHITTENDEN CO.: Hinesburgh, *Hosford, F.H. s.n.*, 22 Sep 1880 (NY,US). FRANKLIN CO.: Fletcher, *Tryon, R.M. 4642*, 14 Oct 1939 (MO). 1+ mi W Fletcher intersect, *Wagner,W.H. & Lellinger, D.B. 9087*, 19 Aug 1959 (MICH). ORANGE CO.: Randolph Center, *Denslow, H.M. s.n.*, 9 Sep 1910 (NY). ORLEANS CO.: 1½ mi S Morgan, Seymour Lake, *Harper, J.S. s.n.*, 31 Aug 1932 (NY). RUTLAND CO.: Rutland, *Eccleston, W.W. s.n.*, 27 Sep 1893 (NY). WINDSOR CO.: Woodstock, Billings Hill, *Kittredge, E.M. s.n.*, 14–23 Sep 1930 (MICH).

WISCONSIN: BAYFIELD CO.: Barnes Twp, Sandbar Lake, *Peck, J.H. s.n.*, 21 Sep 1979 (UWL). Sand lake near Barnes, *Tryon, R.M. 4100*, 14 Jul 1938 (WIS). Sect 31, NW ¼, T 45 N, R 8 W, *Moran, R.C. 125752*, 3 Sep 1980 (MIL). DOUGLAS CO.: Black Fox Lake, *Somerville, M.F. 71*, 20 Sep 1930 (WIS). Cheney Lake, *Somerville, M.F. 47*, 10 Sep 1931 (WIS). Deer Print Lake, *Somerville, M.F. 44*, 20 Sep 1930 (WIS). Gordon, *Somerville, M.F. s.n.*, 1 Sep 1929 (MO). Gordon, 2nd beach sand lake, *Somerville, M.F. s.n.*, 1 Sep 1929 (MICH). Lower Eau Claire Lakes, *Somerville, M.F. 55*, 5 Sep 1932 (WIS). N of sand lake, *Peck, J.H. s.n.*, 17 Jul 1979 (UWL). Sand lake, *Conklin & Somerville 1180–83*, 6 Sep 1938 (WIS), *Fisher, M 79–81*, 17 Jul 1979 (Pigeon Lake Field Station), *Fuller, A.M. 3926*, 6 Aug 1930 (MIL), *Somerville, M.F. s.n.*, 25 Jul 1931 (WIS). Sand lake near Barnes, *Tryon, R.M. 4100*, 14 Jul 1938 (WIS). Sand lake on 2nd beach, *Somerville, M.F. s.n.*, Sep 1938 (MIN). Sand lake, 1st & 2nd beaches, *Conklin & Somerville 109595a*, 6 Sep 1938 (MIL), *1182* (WIS), *1187* (US). Smith Lake, *Somerville, M.F. 49*, 21 Aug 1931 (WIS). 12 mi E Solon Springs, sand lake on county H, *Tryon, R.M. & P.F. 4336*, 4 Jul 1940 (MO). MARINETTE CO.: Near Peshtigo, *Grassl, C.O. 7393*, 2 Sep 1936 (MICH). PORTAGE CO.: N of Almond, *Thomson, J.W. s.n.*, 24 Aug 1938 (WIS). WAUSHARA CO.: Sand lake, *Sorenson 2660*, 17 Jul 1962 (WIS).

Various aspects of the systematic biology of *B. rugulosum* (identified as *B. ternatum*) are dealt with by Wagner (1959, 1960a,b, 1961, 1962a). This is a very rare fern, in spite of the many localities recorded in the range map, Fig. 4. It seems to be most numerous in Vermont and Michigan, but this may be due in part to the intensive collecting in these two states. At the majority of places there are only one or a few individuals, occurring with related species which are much more common. It grows associated with other members of subgenus *Sceptridium*: in its northern occurrences mainly with *B. multifidum* and in its southern occurrences with *B. dissectum*. In Michigan we deliberately set out to discover sites, and invariably we found either *B. multifidum* or *B. dissectum* first and then searched for *B. rugulosum*. We suspect that there are many localities yet to be discovered, especially in southern Ontario, the Upper Peninsula of Michigan, and northern Wisconsin.

Figure 5 presents the results of thorough collecting in 24 places in south-

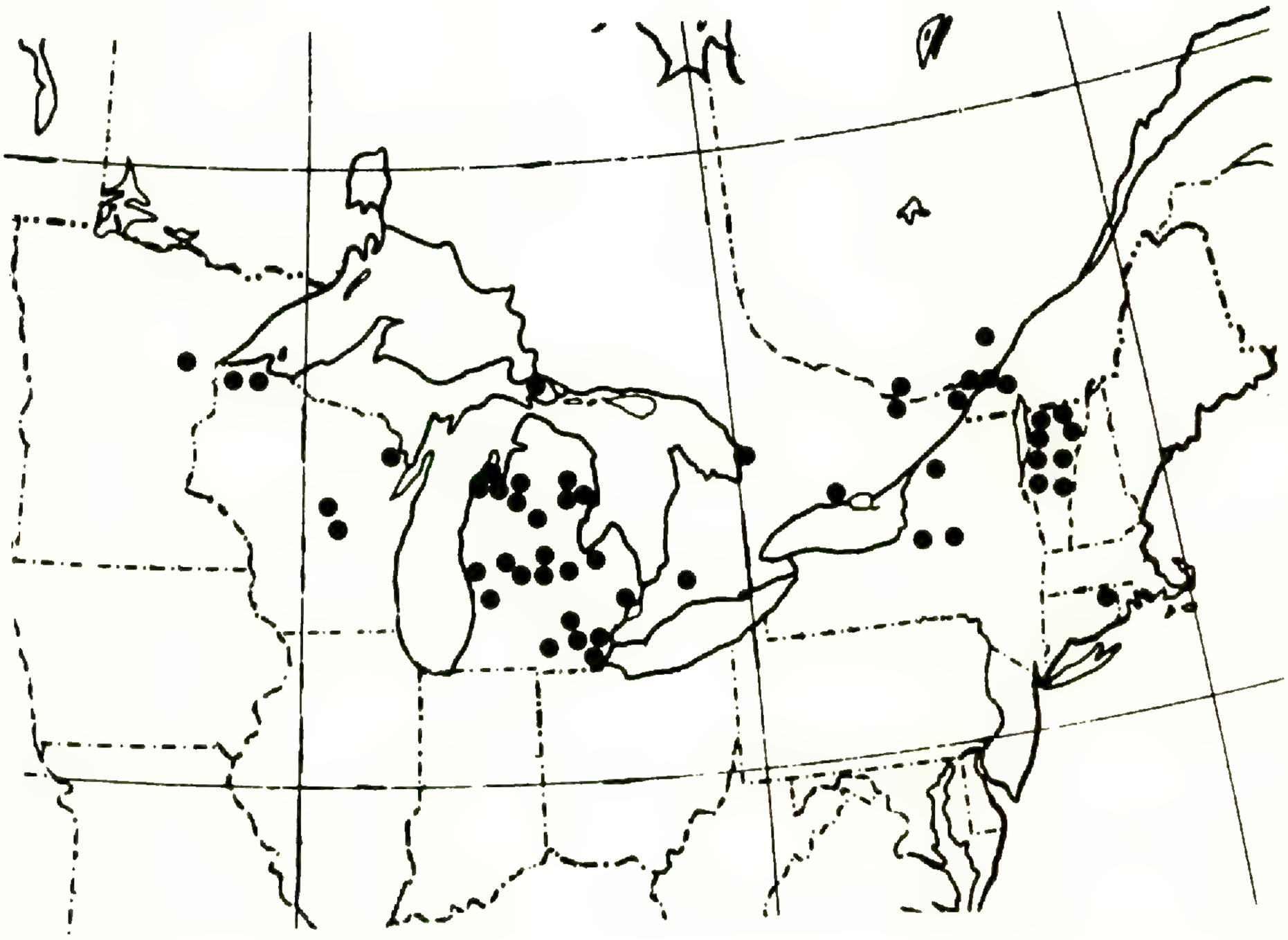

FIG. 4. County distribution map of *Botrychium rugulosum* based on herbarium collections.

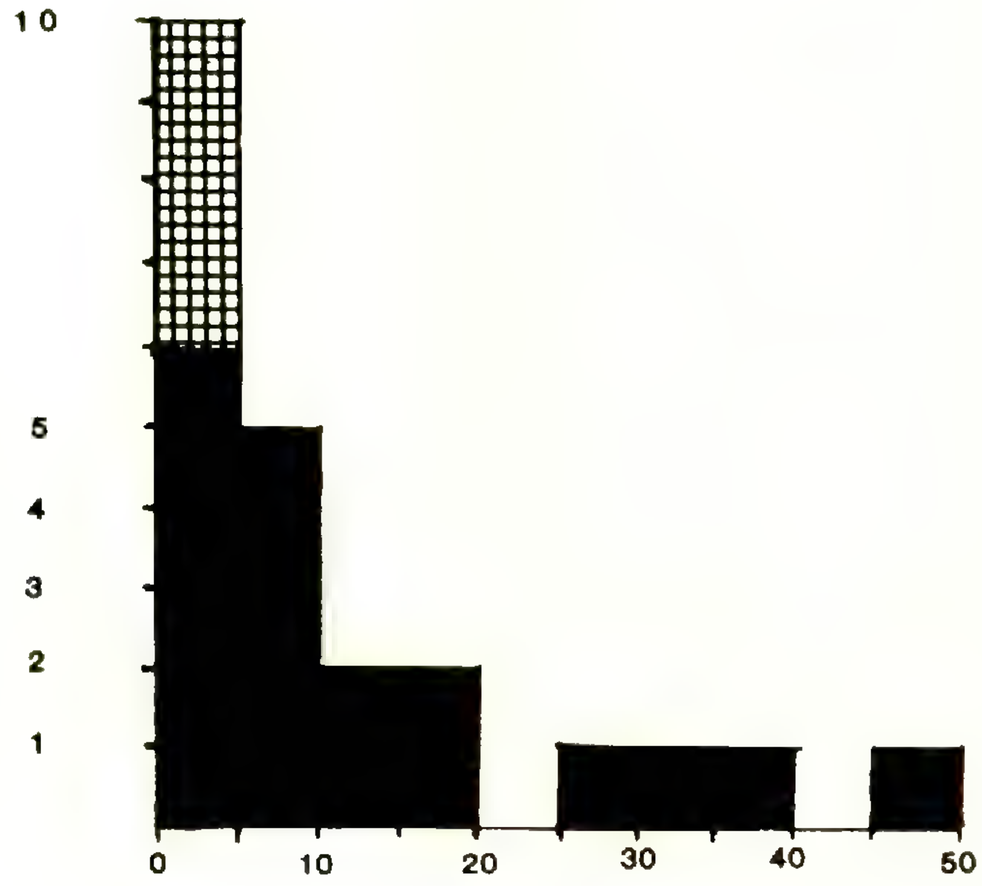

FIG. 5. Bar graph of incidence of plants of *B. rugulosum* in 24 localties in southeastern Michigan. Y axis = number of localities; X axis = no. of plants. (Single locality with 130 plants not shown).

eastern Michigan from Midland County south to Monroe County, and including eight counties altogether. The bar graph gives the number of localities that produced progressively 1–5, 6–10, and so on, plants. The best spot (Monroe Co., 2 mi. n. e. of Petersburg, *W. Wagner 8594,* (MICH)) yielded 130 specimens; it is not shown on the graph. As will be seen, however, most of the habitats gave far less. Indeed, 15 of them had ten or less individuals, 62.5 percent of the total, and 6 (25 percent) (shown in black in first bar) had only one! The survey, which was made over a three-year period (1957–1959), gave results which have since been repeatedly confirmed. This means that if a large stand of evergreen grapeferns of more common species is discovered, it should be carefully examined, for there

may be one or a few *B. rugulosum* mixed in. The median number per locality in our survey was seven, and the mean 17. *Botrychium dissectum* was found in all 24 localities, *B. oneidense* (Gilb.) House in 12, and *B. multifidum* in 11. If our survey had been made in northern Michigan or Wisconsin, *B. dissectum* and *B. oneidense* would probably have been uncommon or absent, and *B. multifidum* would be invariably present.

The substratum in all localities is sandy or silty with more or less included black organic matter. The soil evidently ranges from circumneutral to acidic, more commonly the latter. In the southern portion of the range, *B. rugulosum* is found mostly in low swampy areas, especially in old second-growth grassy places and along paths. Past grazing evidently stimulates the formation of populations. Old apple orchards abandoned for twenty or more years provide productive sites, as do brushy old fields and second-growth upland woods. In Vermont and New York actively pastured open fields and meadows have proved to be ideal and in these places we have frequently been interrupted in our studies by the visits of curious cows. The grazing does not seem to have any serious effects on the plants, although some of them appear trampled and many are dwarfed. The most dwarfed and compact sun forms of *B. rugulosum* and other sceptridiums occur in open, exposed grassy areas around and near borders of sandy lakes as in northern Michigan (especially Grand Traverse Co.) and northern Wisconsin (Douglas Co.), where its most common associate is *B. multifidum*.

In the more northern localities for *B. rugulosum* the haircap moss, *Polytrichum*, is usually abundant, associated with low shrubs such as *Gaultheria procumbens* and *Rubus hispidus*. Other woody plants found with it are generally scattered or clumped, and include *Acer rubrum, Betula papyrifera, Hamamelis virginiana, Populus tremuloides, Prunus serotina, Salix* spp., *Spiraea alba,* and *Vaccinium angustifolium*. Also found are such herbaceous genera as *Antennaria, Fragaria, Hieracium, Lycopodium, Osmunda, Pteridium,* and *Solidago*.

In southern localities (as illustrated in Michigan in the region from Saginaw and St. Clair counties to Monroe Co.), grapeferns grow in richer sites as a rule, and the plants of *B. rugulosum* reach the largest size known, some of the sterile fronds attaining 25 or more cm in length (Wagner, 1959, pl. 9). Associated with the fern in these richer sites are such woody taxa as *Acer rubrum, Cornus drummondii, C. racemosa, C. stolonifera, Corylus americana, Populus tremuloides, Sassafras albidum, Ulmus americana,* and *Vitis riparia*. Among the herbs are species of *Anemone, Aster, Desmodium, Equisetum, Fragaria, Solidago,* and *Viola*. The spleenwort fern, *Asplenium platyneuron,* has in recent years become one of its most frequent associates.

The actively grazed pastures that we studied in Franklin Co., Vermont, and in St. Lawrence Co., New York, contain much more freshly disturbed conditions than the foregoing. The botrychiums tend to be most common in the most open areas, where the cattle trample some and perhaps nibble some. Trees occur mainly at the edges in the less disturbed parts of the pastures. Where grazing is most intense, the plants of *B. rugulosum* may occur in almost lawn-like habitats. Clumped vegetation is produced by *Dennstaedtia punctilobula, Pteridium aquilinum, Rubus idaeus, Comptonia peregrina, Spiraea alba, S. tomentosa,* and *Juniperus virginiana*. Colonies of these species overtop the other vegetation which is made up of such genera as *Achillea, Antennaria, Danthonia, Fragaria, Gnaphalium, Hieracium, Lycopodium, Panicum, Plantago, Poa, Polygonum, Polytrichum, Prunella, Rumex,* and *Viola*.

In localities for *B. rugulosum* we often encounter not only one to three other species of evergreen grapeferns, but the moonworts, *B. matricariifolium* and *B. simplex*, the rattlesnake grapefern, *B. virginianum*, and the northern adder's-tongue, *Ophioglossum vulgatum* var. *pseudopodum*. At the type locality for *B. rugulosum* there were seven species of *Botrychium* plus the *Ophioglossum*. The

seasonal sequence of leaf development in the four species of Great Lakes evergreen grapeferns is in the order (1) *B. multifidum,* (2) *B. oneidense,* (3) *B. rugulosum,* and (4) *B. dissectum* (Wagner 1960, 1961). Leaf development in all of these ferns is exceptionally slow, taking 3–4 months from the time of appearance of the young frond above ground in May or June and the maturation of the leaf and sporangia in September and October. The contrasts are striking in mixed populations in late June and July when the species differ widely in the extent of leaf development. *Botrychium rugulosum* new leaves average 1.3–1.8 times as developed as those of *B. dissectum* during June and July. During the same period the young leaves of *B. multifidum* are approximately 2–4 times further developed than those of *B. rugulosum.* The same phenological differences exist in respect to sporangial maturation in the fall, as measured by the changes in sporangial color from green to yellow to brown, although these changes are more variable than the early vernation changes.

Once a field botanist becomes familiar with the characters of *B. rugulosum* it is unlikely that he will confuse it with any of the three other members of subg. *Sceptridium* that occur in the Great Lakes area. A key to these is given below. Of all the species, *B. rugulosum* has the most slender appearance and a somewhat thinner texture. Although over-all frond size is extremely variable both within and between populations, *B. rugulosum* can be told immediately from *B. dissectum* because it lacks the long undivided terminal segment of the pinna tips (Figs. 2, 3). All of the pinnules of *B. rugulosum* tend to be smaller than those of *B. dissectum* and are usually only one- to two-thirds as large. In the wild the distinctive rugulose and convex pinnule surfaces of *B. rugulosum* are especially valuable in distinguishing it from *B. dissectum.* The bizarre dissected form of *B. dissectum* is connected by intermediates to the "normal" form, f. *obliquum.* Some of the intermediates can occasionally be confused with *B. rugulosum,* unless the pinnule shapes are carefully examined. Even though they may be rather finely cut, the forms of *B. dissectum* always show the outline of the long terminal segments. Those of *B. rugulosum* are not only evenly divided to the tip, but the tips tend to be blunter. *Botrychium rugulosum* is readily separated from *B. multifidum* by its smaller segments; their strongly angular, rather than rounded, outlines (Fig. 3); their rugulose, rather than smooth, surfaces (Fig. 1); and the marked differences in timing of vernation (Wagner, 1960a). Unfortunately the spores of all of these grapeferns are variable, and we have not yet been able to find differences dependable enough to use in routine identification.

The true *B. ternatum* of Japan is a plant of wooded hillsides, pathways, and grassy terraces. It is more finely divided than *B. rugulosum,* and the ultimate divisions tend to be linear, linear-lanceolate, or lanceolate-ovate, with their sides more parallel. The segments are not only narrower, but their margins are beset with delicate, very narrow, pointed teeth, these of very different shape, as a rule, from those of *B. rugulosum.* The texture of *B. ternatum* is generally thinner and more herbaceous than that of *B. rugulosum.* Smith (1967) found in an analysis of their phenolic compounds that *B. ternatum* is more similar to *B. japonicum* (Prantl) Underw., and that *B. rugulosum* is more similar to *B. dissectum. B. ternatum* differs from *B. rugulosum,* according to Smith, in presence or absence of six phenolic compounds.

Of other New World sceptridiums that might be confused with *B. rugulosum* only *B. schaffneri* Underw. of Mexico southward is likely to cause any problems. It is a plant of pine woods and pastures at high altitudes with pinna outlines more narrow and more sharply deltoid than in *B. rugulosum.* The primary pinnules are more contracted basally, and the median and submedian pinna bases are more inequilateral, the basiscopic first pinnule becoming nearly sessile on the rachis, the acroscopic first pinnule remote from the rachis. The sterile segments of *B. schaffneri* are slightly more divided, the ultimate pinnules more distant, smaller, and commonly unequally bifid with the acroscopic lobe larger.

Chemical evidence found by Smith (1967) indicates closer relationship of *B. schaffneri* to other southern and tropical American taxa (*B. lunarioides* (Michx.) Sw. and *B. jenmanii* Underw.) than to any other botrychiums.

DISCUSSION

Botrychium rugulosum is unquestionably a distinct species, and the combination of its geographical range, periodicity, blade cutting, segment shapes, laminar contours and marginal teeth set it apart from all other species of subg. *Sceptridium*. The populations of *B. rugulosum* are consistent in repeating the specific characters uniformly in over 70 localities in an area of the Great Lakes region that extends approximately 1000 miles (1600 km) from Minnesota in the west to Connecticut in the east. Most importantly, *B. rugulosum* grows intermixed with other sceptridiums in the same habitats. It exists side-by-side with *B. dissectum* and *B. multifidum* and sometimes *B. oneidense* as well. The distinctive characters of *B. rugulosum* are therefore not merely environmental modifications.

It is intriguing to speculate on the origin of this species. How is it possible for a species to be limited to an area that 15,000 years ago was completely covered by Wisconsin glaciation? We might also ask the same question about the rare and local little goblin fern, *B. mormo* W. Wagner, of northern Michigan, Wisconsin, and Minnesota (Wagner & Wagner, 1980). There are a number of possible hypotheses to explain these ranges. Among them we can propose explanations invoking (1) long-distance dispersal, (2) allopatric speciation, (3) relicts, and (4) migration.

As to long-distance dispersal by spores, our original idea that *B. rugulosum* was actually the same as the Asiatic *B. ternatum* is now abandoned and an assumption that we had received this species in the New World from spores carried by prevailing winds from the west is now without support. We know of no place in the world today, other than the Great Lakes region, where there are plants that conform to *B. rugulosum*. The second hypothesis involving *de novo* evolution of a new species following glaciation also seems questionable. It is difficult for us to imagine a new species of *Botrychium* based on a number of characters (Wagner 1960b) evolving as a result of temporarily localized allopatry independent of its relatives, and then quickly spread over such a wide range.

The hypothesis that *B. rugulosum* may represent a relict that survived in non-glaciated areas does not seem unreasonable, but there is as yet scanty evidence of the role of refugia. The classical idea of nunataks, for example, has usually been contradicted by substantial geological data. On the other hand, *B. rugulosum* may have survived glaciation in, for example, the Driftless Area of Wisconsin, and when the glacier receded and the climate changed, the fern returned eastward and northward to its present range.

To us, the hypothesis of migration southward with the glacial front is at present the most appealing. Recent phytogeographers are inclined to believe that our northern flora was in general shifted southward by glaciation and that, ideed, many if not most species were forced into the middle and southern states. Support for this hypothesis comes largely from pollen core data. If *B. rugulosum* had actually been an ancient northern species that migrated southward at the leading edge of the glacier and then later returned, this picture would not be different from that of numerous well known species, especially of trees.

It is interesting to speculate that *B. rugulosum* may have had something to do with the variation of the enigmatic grapefern, *B. dissectum,* and its origin. The northern *Botrychium rugulosum* might have been forced, during glaciation, into contact with the southern *B. biternatum* that today occurs from the Ohio Valley southward to the Gulf Coast. In some ways *B. dissectum* appears to be intermediate between *B. rugulosum* and *B. biternatum*. Perhaps *B. dissectum* constitutes a

more or less stabilized hybrid swarm at the diploid level. Toward the north it is more similar to *B. rugulosum* and toward the south *B. biternatum*. However, even without f. *dissectum*, *B. dissectum* is considerably more variable than either of them. *B. dissectum* f. *obliquum* would represent the "normal" form of the hybrid and the striking and unique f. *dissectum* with its curiously lacerate pinnules might represent the result of morphogenetic upsets due to genetic conflicts (cf. Wagner, 1962b).

KEY TO GREAT LAKES BOTRYCHIUM SUBG. SCEPTRIDIUM

1. Sterile pinnules deeply and conspicuously lacerate, the ultimate segments linear or narrowly oblong, with mostly 1–2 veinlets. *B. dissectum* f. *dissectum* (intergrades to *B. d.* f. *obliquum*)
1. Sterile pinnules dentate to entire, not lacerate, the ultimate segments wider, mostly ovate, spatulate, or lanceolate, with numerous veinlets.
   2. Terminal pinna divisions more or less undivided, linear lanceolate to ovate; plants becoming more frequent south of 43° N.
      3. Plants of various habitats; terminal pinna blades elongate, linear-lanceolate to lanceolate, acute; lamina exposed in winter tending to become bronzy; roots dominantly dark and corky, av. 2.5 mm thick (dried) 1 cm from stem; new leaves appearing in early June. *B. dissectum* f. *obliquum*
      3. Plants of low, shaded forests and swamps; terminal pinna blades ovate-lanceolate to ovate, rounded; lamina exposed in winter remaining dull green; roots dominantly ivory- to tan-colored, smooth, av. 2.0 mm thick (dried) 1 cm from stem; new leaves appearing in middle May. *B. oneidense*
   2. Terminal pinna divisions regularly divided to the tips, plants becoming more frequent north of 43° N.
      4. Pinnules rounded, larger, mostly 4–8 mm wide; the living lamina flat; pinnule margins mostly finely crenate to entire; new leaves appearing in early May. *B. multifidum*
      4. Pinnules angular, smaller, mostly 2–5 mm wide; the living lamina convex and rugulose; pinnule margins mostly coarsely dentate; new leaves appearing in late May. *B. rugulosum*

ACKNOWLEDGMENTS

We are grateful to the many individuals who helped us in the field, the herbarium curators who lent us specimens, and those persons who provided us relevant information about where these plants might occur. We thank David J. Bay and Joseph M. Beitel for their help with the illustrations, and we give special thanks to Kerry S. Walter for his aid in providing computer programs for collection data. W. R. Anderson translated the diagnosis into Latin. This research was carried out in large part under NSF Grant DEB 8005536 for Evolution and Systematics of *Botrychium*.

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OBSERVATIONS ON FOUR SPECIES OF DELESSERIACEAE (RHODOPHYTA) FROM THE SOUTH SANDWICH ISLANDS, THE ANTARCTIC

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A collection of sublittoral benthic marine algae from the South Sandwich Islands in the South Atlantic was recently sent to me by Dr. M. A. Hoban of Texas A & M University. The collection was made by trawl on 30 Sept., 1978, at Zavodovski I. (56°19.5′S; 27°34.5′W), the northernmost island of the archipelago, which is the only active volcanic arc in Antarctic regions. These islands occupy an intermediate location between sub-Antarctic South Georgia and the maritime Antarctic region of the South Orkney Islands, and the terrestrial vegetation is essentially Antarctic in character (Longton & Holdgate, 1979). The South Sandwich Islands lie in the Low Antarctic province of Wace (1965) and are situated south of the Antarctic Convergence.

Although Kemp & Nelson (1931) reported that some brown and red algae were collected by trawling by a British expedition on board R.R.S. 'Discovery' and that the kelp *Macrocystis pyrifera* was conspicuously absent, the only other prior marine algal collection from these islands was that reported by Zinova (1966), who listed 8 species, none the same as those reported here.

Numerous specimens of 4 species of Delesseriaceae were contained in the present collections, and they are known from only a few records in the literature.[1] These species, *Delesseria salicifolia* Reinsch, *Microrhinus carnosus* (Reinsch) Skottsb., *Neuroglossum ligulatum* (Reinsch) Skottsb., and *Phycodrys austro-georgica* Skottsb., were all originally described from South Georgia, 470 km to the NW. Two of them, *D. salicifolia* and *N. ligulatum*, have been reported only from that island. Moe and DeLaca (1976) reported *Microrhinus carnosus* from the South Shetland Is. and *Phycodrys austro-georgica* from the South Shetland Is. and the Antarctic Peninsula.

The present paper provides new information about the vegetative and reproductive morphology of these species and discusses their taxonomic placement within the family Delesseriaceae. Evidence is presented demonstrating that *Delesseria stephanocarpa* (A. & E. S. Gepp) Skottsb., a species that has been recorded north to 47° S latitude on the Argentine coast, should be included with *D. salicifolia*. Representative specimens of the four species have been deposited in the University of Michigan Herbarium (MICH).

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[1]It should be inserted that the records of all these species from the "Argentine littoral" by Pujals (1963) and Kühnemann (1972) are not from the Argentine mainland proper but from the Antarctic and sub-Antarctic islands. Thus, they do not represent new records except for that of *Delesseria stephanocarpa* by Kühnemann (1969).

Delesseria salicifolia Reinsch (Figs. 1–9).
Syn.: *Delesseria stephanocarpa* (A. & E. S. Gepp) Skottsb.

Reinsch (1888) described *D. salicifolia* from S. Georgia and later (1890) provided illustrations to show a much branched *Delesseria* composed of blades 4–11 cm long and 11–16 mm wide bearing well developed opposite nerves and with special tetrasporophylls only 2–3 mm long that develop from the midrib. Reinsch pointed out that outwardly it resembled *D. lyallii* [= *Cladodonta lyallii* (Hook. f. & Harv.) Skottsb.] except in the character of the margin, but in regard to its production of special tetrasporophylls from the midrib it agreed with *D. sanguinea*.

Kylin and Skottsberg (1919) later re-recorded this species from S. Georgia and included a photograph of a small tetrasporophyll with serrate margins. They also stated that cystocarpic plants were not known in this species and called attention to the possibility that *D. stephanocarpa* could very well represent the female plant of this species. Subsequent authors (Skottsberg, 1923, 1941, 1953; Papenfuss, 1964) did not refer again to the possible connection. *Delesseria stephanocarpa* was described (as *Hydrolapathum stephanocarpum*) by Gepp & Gepp (1905, 1912) from the South Okney Is. The Gepps stated that their species was "most nearly related" to *D. sanguinea* but differed in having cystocarps decorated with simple outgrowths, forming a "wreath of appendages." They referred to the blades of their alga as having conspicuous veins and having a width of 3–4 mm. Skottsberg (1941), who transferred it to *Delesseria*, said that it was related to *D. sanguinea* and *D. fuegiensis*. Its distribution was extended to western Antarctica and the South Shetland Is. by Skottsberg (1941) and Moe and DeLaca (1976). It had also been recorded from the Argentine mainland at Puerto Deseado, at 47°45′ S lat. (Kühnemann, 1969).

The material from Zavodovski I. includes both tetrasporic and cystocarpic specimens. Individual blades range from 4 mm to 8 or more mm in width; one older blade measured up to 18 mm in width. This range overlaps the values given for *D. salicifolia* and *D. stephanocarpa*. The margins of the blades are entire and slightly undulating. A well developed midrib is present. Lateral veins are simple and extend almost to the margins in mature blades. Blades are densely branched from the midrib. Wings (= alae) are monostromatic, except for the veins. Sections of midribs of mature blades showed rhizoidal cells intermingled with large cells (cf also Skottsberg, 1923), a structural arrangment distinguishing *Delesseria* from *Apoglossum*, in which a sheath of rhizoidal cells encircles a layer of large cells (Kylin, 1956).

Tetrasporangia and procarps are produced on small special leaflets arising from the midrib. The tetrasporophylls are 1000–1200 μm long and 600–700 μm wide and have serrate margins (Figs. 7–9), agreeing with the description of *D. salicifolia* by Skottsberg (in Kylin & Skottsberg, 1919). Female leaflets are 800–1000 μm long and 400–500 μm wide at the time that early post-fertilization stages are discernible. These female leaflets also have serrate margins, and small spine-like processes develop on the young pericarp (Figs. 1–4). The mature cystocarpic proliferations are 2–4 mm long, and numerous elaborate appendages or spines cover the pericarp (Figs. 5 & 6). Comparably adorned cystocarps occur in two other delesseriacean species, namely, *Polyneura hilliae* (Grev.) Kyl., in which a mass of spines cover the pericarp (Kylin, 1924), and *Zinovaea acanthocarpa* Wynne, in which spiny membranous extensions course over the pericarp (Wynne, 1970).

The most significant point concerning the close similarity between the female and tetrasporic bladelets is that they complement the vegetative similarities existing between *D. salicifolia* and *D. stephanocarpa* and necessitate the conclusion that a single species is involved, a possibility first suggested by Kylin and

Skottsberg (1919). *Delesseria salicifolia* appears to be distinct from the 9 other species of *Delesseria* listed by Papenfuss (1964) from the Antarctic and Sub-Antarctic. Most of these species are not well known, but two, *D. fuegiensis* Skottsb. and *D. macloviana* Skottsb., were recently studied in some detail (Mendoza, 1974). Cystocarps in both species are unornamented, and venation is less pronounced than in *D. salicifolia*. Cystocarps are also unornamented in *D. lancifolia* (J. D. Hook.) J. Ag. (Skottsberg, 1923) and in *D. belayevii* Zinova (Zinova, 1963).

Microrhinus carnosus (Reinsch) Skottsb. Figs. 10–18.

Microrhinus is a monotypic genus that was established by Skottsberg (1923) on the basis of *Delesseria carnosa* Reinsch (1888) described from S. Georgia. Skottsberg (in Kylin & Skottsberg, 1919) initially transferred Reinsch's alga to *Chauvinia* Harv. (presently *Chauviniella* Papenfuss, 1956) but subsequently recognized it as a distinct genus, since its apex did not conform to that pattern typical of the *Hypoglossum* group of Kylin (1924), to which *Chauviniella* is assigned. Other characteristics of *Microrhinus* include a polystromatic blade with pronounced midrib, production of female and tetrasporangial reproductive organs on small special bladelets, and the occurrence of these bladelets in clusters arising not only from the region of the midrib but also from the blade margin and randomly over the blade surface. As Skottsberg remarked, the manner in which both vegetative and reproductive proliferations sprout in clusters from the midrib, margins, and surface of the blades makes *M. carnosus* an easily recognizable alga. Simple lateral veins, extending almost to the margins, are visible in younger blades, but these veins are obscured in the thickened older blades.

Reinsch (1890 Pl. VII, fig. 6, Pl. VIII) did not observe reproductive stages, and Kylin & Skottsberg (1919) did not discuss reproduction other than to indicate that female and tetrasporic thalli were collected, but later (1923) described female and tetrasporic stages upon establishing the genus. His illustrations included early stages of cystocarpic development. The several specimens in the present collection consist of female/cystocarpic and tetrasporic thalli.

Examination of the apex of very small bladelets revealed a pattern of the *Delesseria* type (Figs. 16–18), in which intercalary cell divisions occur in the second-order cell rows rather than that of the *Membranoptera* type, in which intercalary cell divisions are absent. Skottsberg (1923) had referred to the apex as being the *Delesseria* type, although his figures showed no intercalary divisions in the second-order cell rows. He stressed its resemblance to another polystromatic alga, *Pantoneura*, and Kylin (1924) assigned *Microrhinus* to the *Membranoptera* group because of its resemblance to *Pantoneura*, one of the members of that group.

The consequent transfer of *Microrhinus* from the *Membranoptera* group to the *Delesseria* group necessitates a re-examination of the genera within that group. It currently contains the following genera: *Delesseria, Apoglossum, Marionella, Laingia, Pseudolaingia, Yamadaphycus,*[2] and *Odontolaingia*, which was recently described by Mendoza (1976). Of these 7 genera only *Yamadaphycus*

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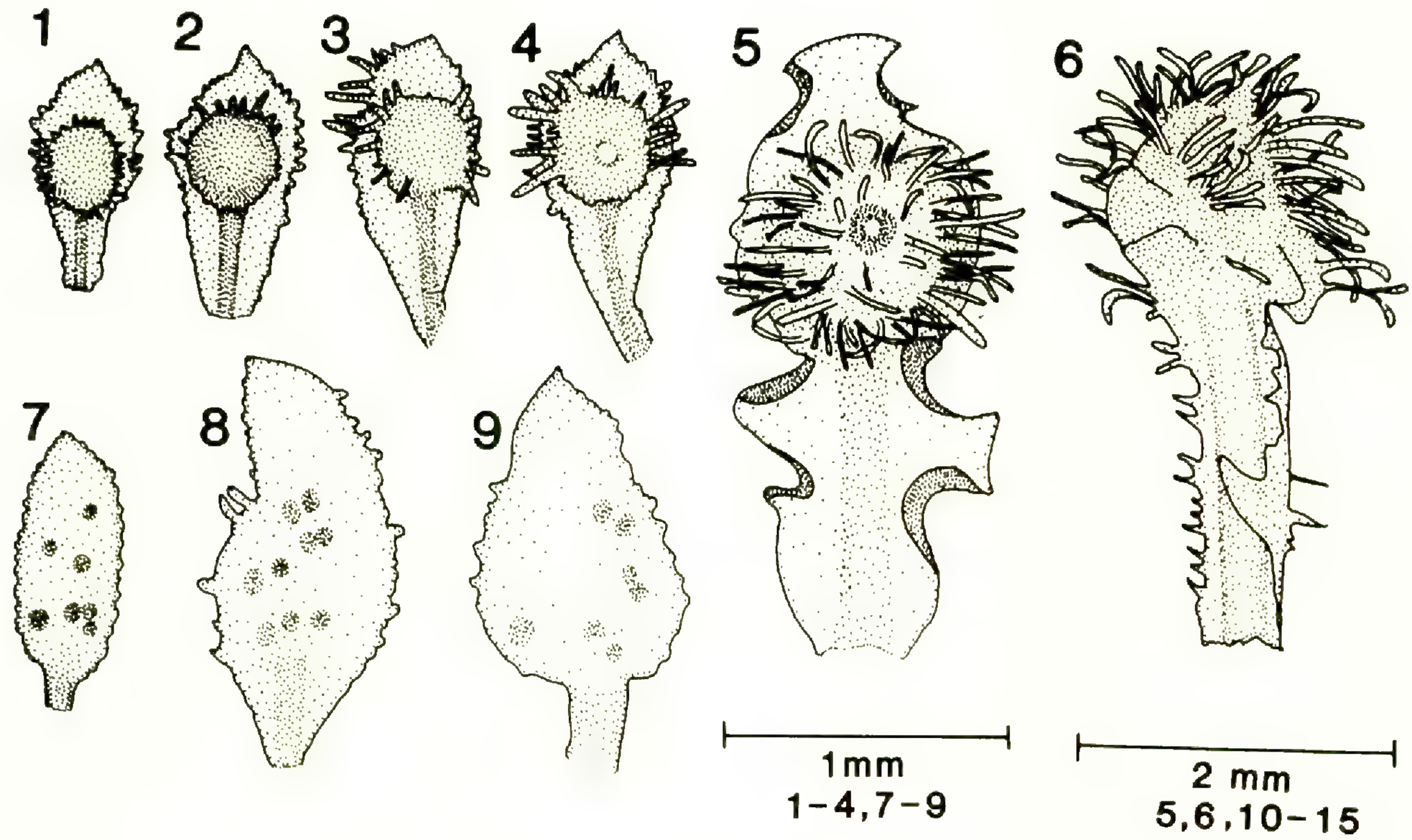
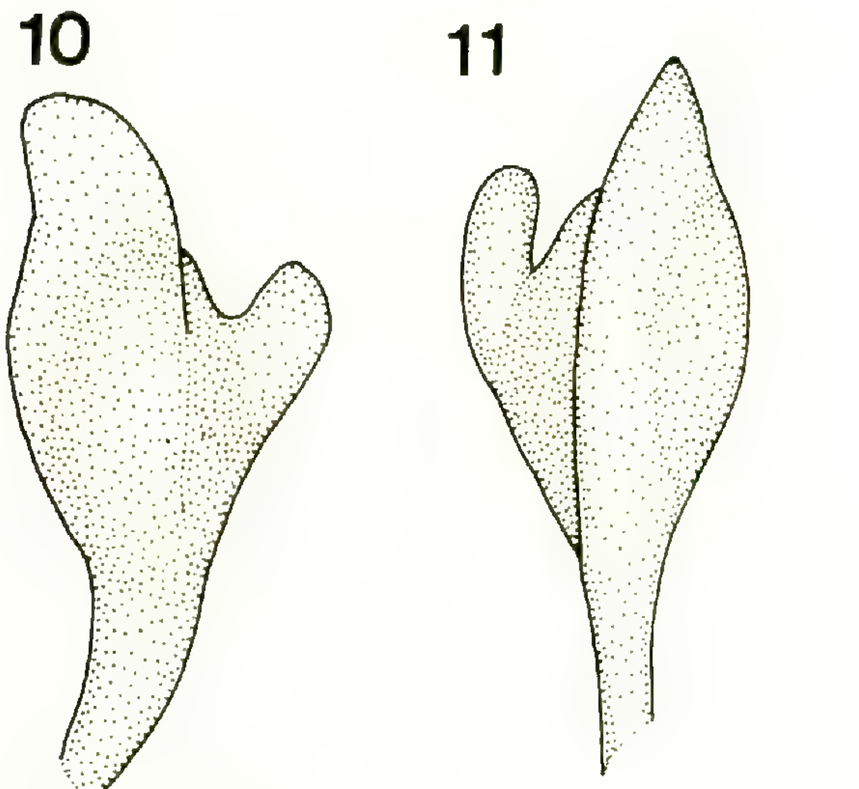
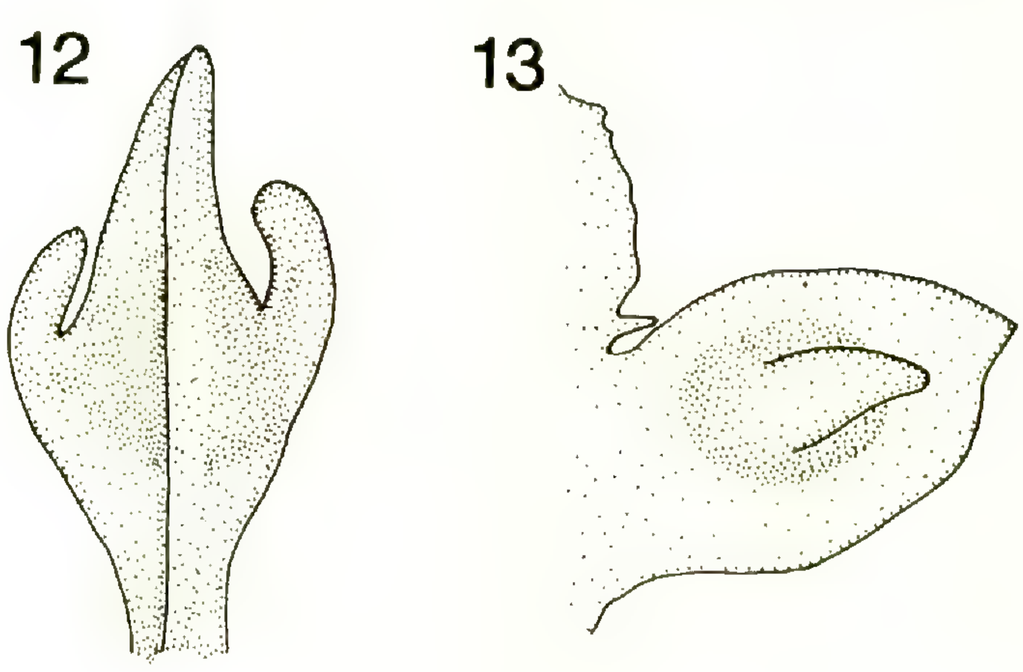
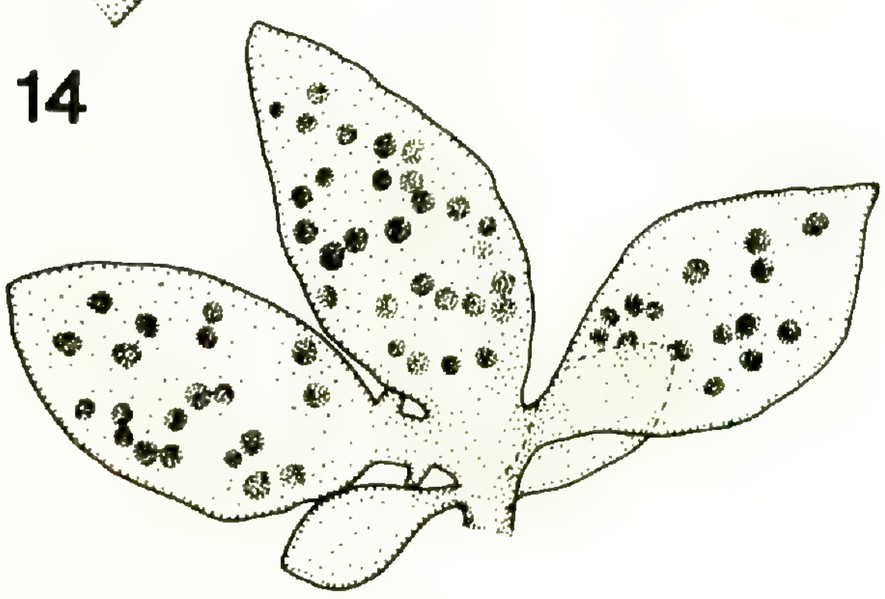
[2]Whether *Okamurina* (Zinova, 1972) or *Yamadaphycus* (Mikami, 1973) is the correct name of this genus has become confused. Recently Mikami and Yoshida (in Yoshida, 1980) adopted the name *Okamurina*. However, because Zinova (1972) based her genus *Okamurina* on *Laingia pacifica* Yamada (Yamada, 1932) [actually *Pseudophycodrys pacifica* Yamada, 1930], which had already been used as the type of Mikami's genus *Congregatocarpus* (Mikami, 1971b), on the basis of Article 63 of the International Code of Biological Nomenclature (Stafleu *et al.*, 1978) *Okamurina* must be regarded as nomenclaturally superflous and thus illegitimate. Zinova's (1976) later move to rectify the situation is inadmissable. Therefore, the correct name of this genus is *Yamadaphycus*.









FIGS. 1–15. Figs. 1–9 *Delesseria salicifolia*; Figs. 10–15 *Microrhinus carnosus*. Figs. 1–4, young stages of developing cystocarps on special leaflets; Figs. 5 & 6, mature cystocarps on special leaflets; Figs. 7–9, special leaflets bearing tetrasporangia; Figs. 10–13, special leaflets bearing cystocarps (10–12 are leaflets arising from blade surface; 13 is a leaflet arising from blade margin); Figs. 14 & 15, clusters of special leaflets bearing tetrasporangia, the stipes proliferating new leaflets.

seems similar enough to warrant comparison. There are strong similarities between *Yamadaphycus* and *Microrhinus* beyond the coincidental sharing of the epithet 'carnosus.' Both have coarse, polystromatic blades, and cystocarps and tetrasporangia are produced on special proliferations, usually in clusters that are scattered over the entire blade surface. New blades arise both from the midrib

and also from the blade margins. Midribs are present in both genera. Lateral venation is evident in both genera, although in *Yamadaphycus* it is "often inconspicuous" (Mikami, 1973) and in *Microrhinus* not visible in older blades. One apparent difference is the arrangement of tetrasporangia on the special proliferations. Zinova (1972) described the tetrasporangia as occurring in rows on the sporophylls. Such a pattern, however, is not evident in Mikami's (1977, fig. 8) figure of a mature tetrasporophyll nor in a specimen of this species deposited in the University of Michigan Herbarium and determined by H. Mikami. Tetrasporangia are randomly arranged on the tetrasporophylls of *Microrhinus* (Figs. 14 & 15).

Skottsberg (1923) stated that in *Microrhinus* new sporophylls arise from the stipes of older ones and that this process can be repeated, resulting in a dense tuft of leaflets. In *Yamadaphycus* the tetrasporic proliferations radiate from a central core or base (Mikami, 1971a; Zinova, 1972). The tetrasporophylls of *Yamadaphycus* measure 1.5–2.5 mm in length and 0.5–0.1 mm in width (Mikami, 1977), whereas the average size of those of *Microrhinus* was reported by Skottsberg (1923) to be 4–5 by 3 mm. Much variation in size of tetrasporophylls (and cystocarpic proliferations), however, was observed in the Zavodovski I. material. Many tetrasporophylls are 1.5–2.5 mm long and about 1.2 mm wide, as Figs. 14 & 15 represent; but some tetrasporophylls are up to 5 mm long and 3 mm wide, agreeing with the average values given by Skottsberg. The overlap in size of tetrasporophylls between these two taxa is obvious.

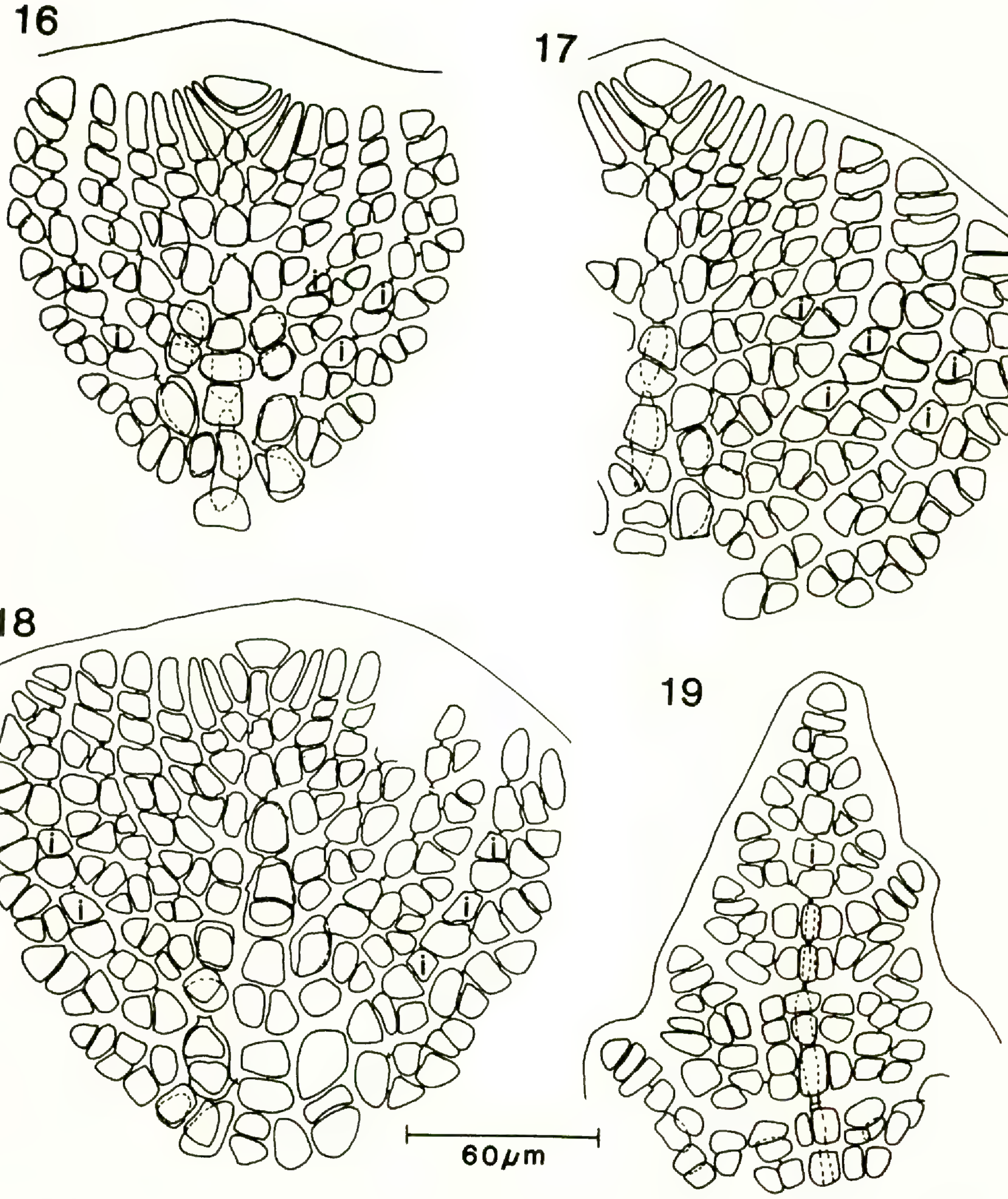
Cystocarpic proliferations demonstrate some differences. Although dimensions of the bladelets are similar, the apices are attenuate or mucronate in *Yamadaphycus* but rounded in *Microrhinus*. Furthermore, ostioles of *Microrhinus* are provided with the prominent curved beak (Figs. 10–12; Skottsberg, 1923), whereas those of *Yamadaphycus* are simple. A single cystocarp is borne per bladelet in *Yamadaphycus*; usually one but less commonly two cystocarps are borne per bladelet in *Microrhinus* (Fig. 12). Carposporangia are produced in chains in both genera.

In summary, the present observations call for the transfer of *Microrhinus* from the *Membranoptera* group to the *Delesseria* group and point out the strong resemblance to *Yamadaphycus carnosus*. My interpretation is that these two taxa (one occurring in the South Atlantic and the other occurring in the northwestern North Pacific) are closely related but can be distinguished on features of the cystocarpic proliferations and the arrangement of tetrasporangia, i.e., allegedly in distinct rows in *Yamadaphycus* but irregularly arranged in *Microrhinus*. In my opinion there is a strong likelihood that the differences cited warrant separating these taxa at only the specific level rather than at the generic level.

Phycodrys austro-georgica Skottsb. Figs. 19–29.

This distinctive species was established by Skottsberg (1923), who described and illustrated sori of tetrasporangia as developing in the swollen lateral nerves of blades and also in special proliferations that arise from the midrib. Skottsberg described but did not illustrate cystocarps. Justification for placing this species in *Phycodrys* came from its *Phycodrys*-type apical growth (Fig. 19; cf. fig. 15c in Skottsberg, 1923), in which intercalary divisions occur in the primary cell row and opposite secondary cell rows are developed equally rather than alternately, the monostromatic nature of the blades (except for the midrib and nerves), and the structure of the midrib. The blades of *P. austro-georgica* have a conspicuous midrib. The lateral veins are macroscopic and become branched in older blades. Blades have marginal dentations, which are outgrowths of the second-order cell rows.

The unusual feature of this species is the dense proliferation of vegetative



FIGS. 16–19. Figs. 16–18 *Microrhinus carnosus*, camera-lucida drawings of apical region of blades; *i* = cells derived from intercalary cell divisions in second-order cell rows; Fig. 19 *Phycodrys austro-georgica*, camera-lucida drawing of apical region, showing the result of an intercalary division in the primary cell row (*i*).

branches from the midrib, or from the remaining rachis of denuded blades, resulting in a shaggy appearance of this alga. The only other species in the genus which has secondary vegetative blades arising from the primary blade surface is *P. amchitkensis* (Wynne, 1970), but the degree of such branching is minimal in that species compared to that in *P. austro-georgica*. It is known that in older specimens of *P. rubens* (L.) Batt., the type of the genus, fertile leaflets (tetrasporic and cystocarpic) can develop from the midrib, lateral nerves, and lamina (Turner, 1808, pl 35; Kylin, 1923, fig. 43d), although vegetative blades do not arise from these areas. The production of vegetative blades would not seem to be such a departure as to exclude *P. austro-georgica* from this genus. Also, a counterpart situation can be cited in the genus *Membranoptera*, another delesseriacean genus with typically only marginal branching. *Membranoptera dimorpha* Gardn.

(Gardner, 1926; Abbott & Hollenberg, 1976) has abundant branching from both the blade margins and the midrib regions, and it continues to be accepted as a *Membranoptera* (Widdowson, 1974; Phinney, 1977; Hawkes *et al.*, 1978). I conclude that it is most reasonable to include this species, *P. austro-georgica*, within *Phycodrys*.

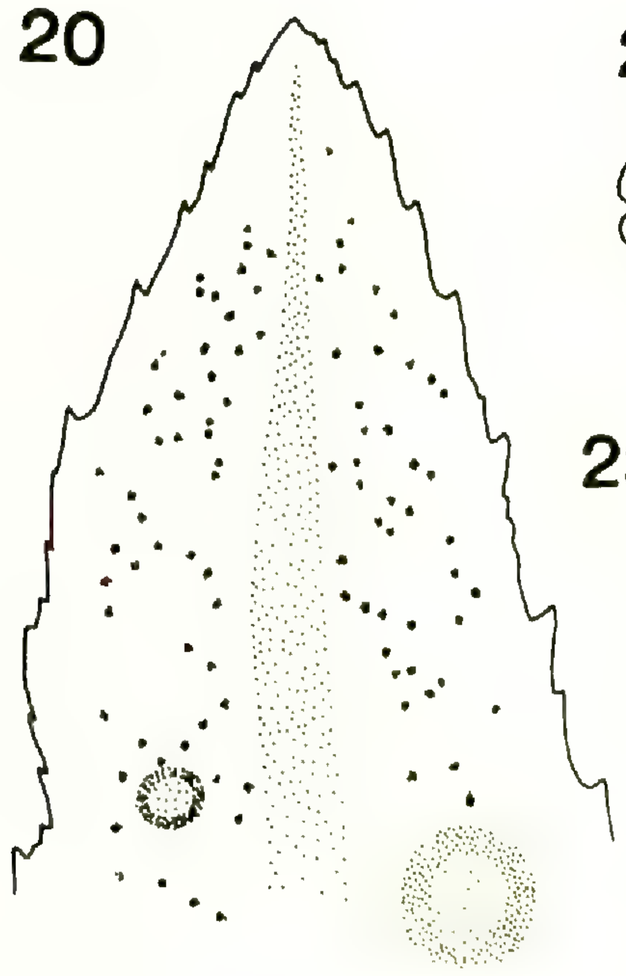
Procarps are randomly scattered over the blade surface (Fig. 20), as is typical of the subfamily Nitophylloideae, and many cystocarps can develop on a given blade. The procarp conforms to the *Phycodrys*-type (Kylin, 1924), which is characterized by a single carpogonial branch associated with two sterile-cell groups, one consisting of usually 4 to 6 cells and the other of 2 or 3 cells. The mature, unfertilized procarp of *P. austro-georgica* commonly has one sterile-cell group composed of 4 cells and the other sterile-cell group composed of two cells (Figs. 21–25).

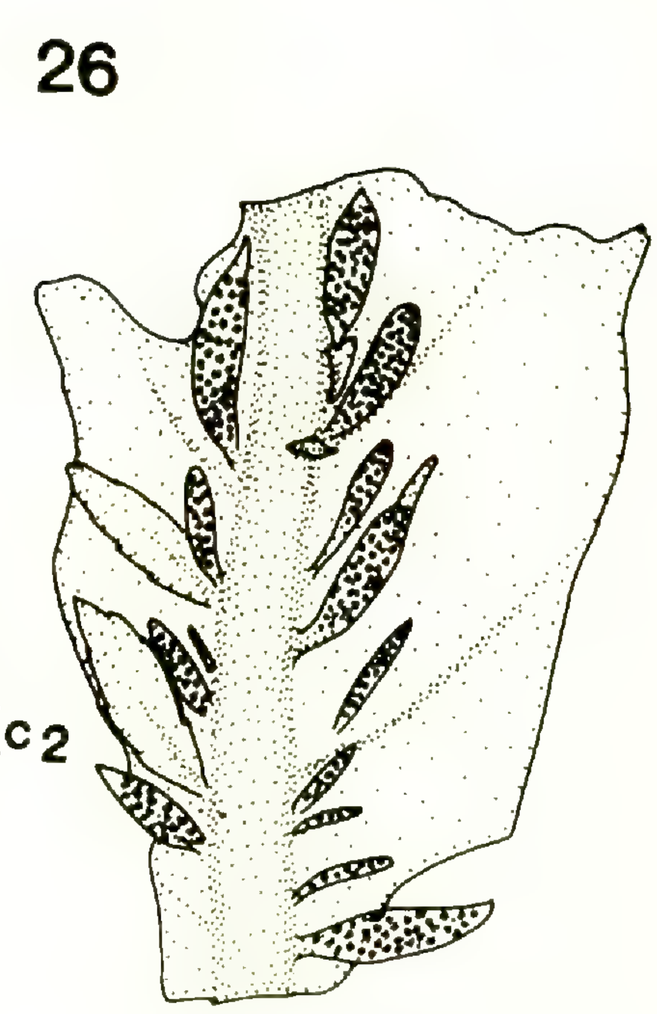
Tetrasporic plants produce tetrasporangia both in discrete swollen sori located at the ends of lateral nerves or blades (Fig. 27) or in small leaflets arising from the sides of the midrib (Fig. 26). Male plants produce spermatangia in leaflets also arising from the midrib (Fig. 28) and completely covering the surfaces except for the margins. Cortical cells produce spermatangial mother cells, the latter cutting off the spermatangia (Fig. 29).

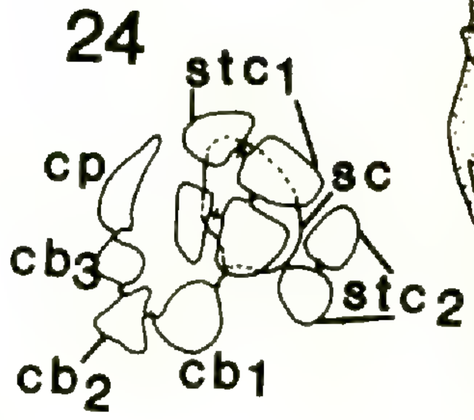
The current status of species within the genus *Phycodrys* deserves some attention. Dawson (1962) compiled a "tentative working key" to the species of *Phycodrys*, which contained 14 species, including 4 new ones. That list should be modified by the following points. *Phycodrys bullata* Gardn. is the basionym of *Tokidadendron bullata* (Wynne, 1970). A second species, *P. ambigua* Gardn., was also transferred to that genus but should be regarded as a synonym of the former species in that it represents a first-year blade of this perennial algae (unpubl. obs.). *Phycodrys elegans* Setch. & Gardn. is a member of the subfamily Delesserioideae and thus should be excluded from *Phycodrys* (unpubl. obs.). The correct name for *P. sinuosa* (Huds.) Kuetz. is *P. rubens* (Dixon, 1964). Taxa that have been described subsequent to Dawson's key are *P. cerrateae* (Dawson *et al.*, 1964), *P. isabellae* (Norris & Wynne, 1968), *P. amchitkensis* (Wynne, 1970), and *P. polycarpa* and *P. pumila* (Zinova, 1972). Taxa omitted from Dawson's account are *P. radicosa* (Okam.) Yamada & Inagaki and *P. rossica* (Sinova) Zinova (Zinova, 1955). Although Dawson included *P. fimbriata* (de la Pyl.) Kyl. in his tally, Atlantic records of that species are commonly treated as *P. rubens* (Taylor, 1962), while records of *P. fimbriata* from the Pacific Ocean (such as Nagai, 1941; Zinova, 1955; Mikami, 1972) have more recently been recorded as *P. riggii* Gardn. (Perestenko, 1980). Likewise, Perestenko (1980) has placed *P. serratiloba* (Rupr.) Zinova (Zinova, 1965) within the synonymy of *P. riggii*. Therefore, a total of 17 species of *Phycodrys* are presently recognized.

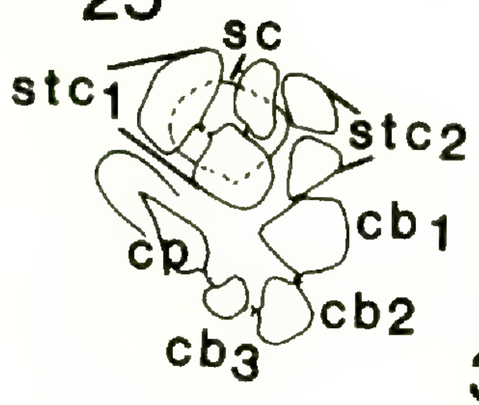
Neuroglossum ligulatum (Reinsch) Skottsb. Figs. 30–37.

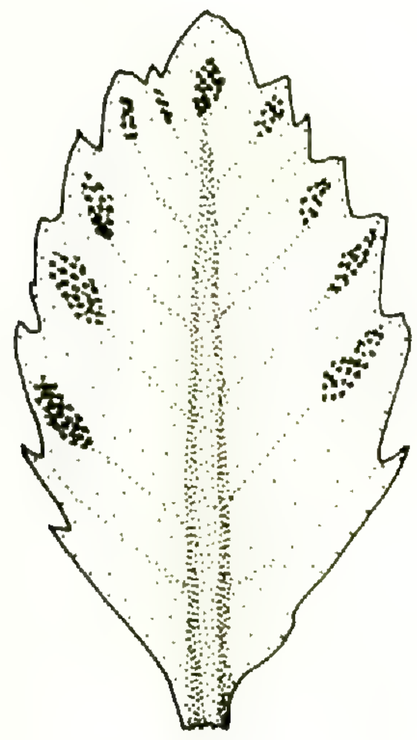
This species is placed in a Southern Hemisphere genus containing 3 species: *N. binderianum* Kuetz., the type, occurring in South Africa; *N. multilobum*, restricted to Tristan de Cunha in the South Atlantic (Baardseth, 1941), and *N. ligulatum*, hitherto known only from South Georgia. Wagner (1954) studied the type species in some detail. *Neuroglossum ligulatum*, on the other hand, is known only from the original description (Reinsch, 1888, 1890), from a few figures of details contributed by Skottsberg (1923), and from Zinova's (1966) report of a cystocarpic specimen from S. Georgia. A photograph now in MICH taken by Dr. W. R. Taylor of a specimen in Skottsberg's collection at the University of Uppsala shows an alga collected by K. A. Andersson at Possession Bay (Stat. 17), S. Georgia, and identified by Skottsberg as *N. ligulatum*. The photograph shows many ligulate blades arising from the midribs of two eroded axes. Lateral nerves

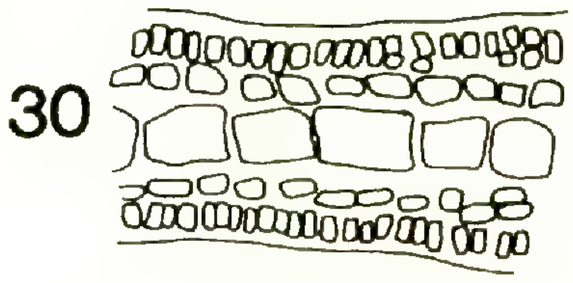


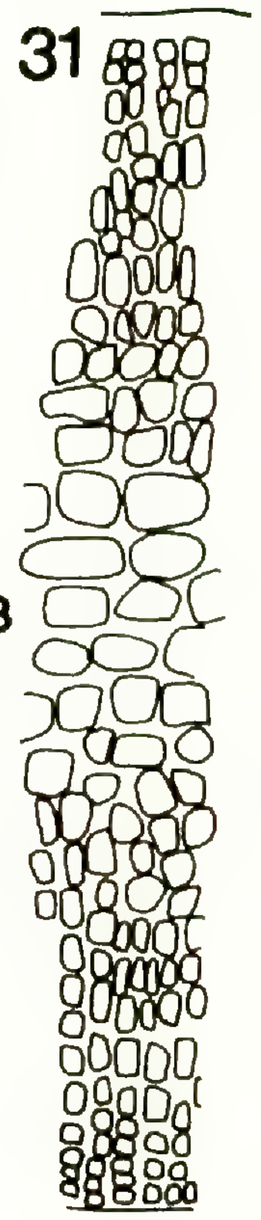


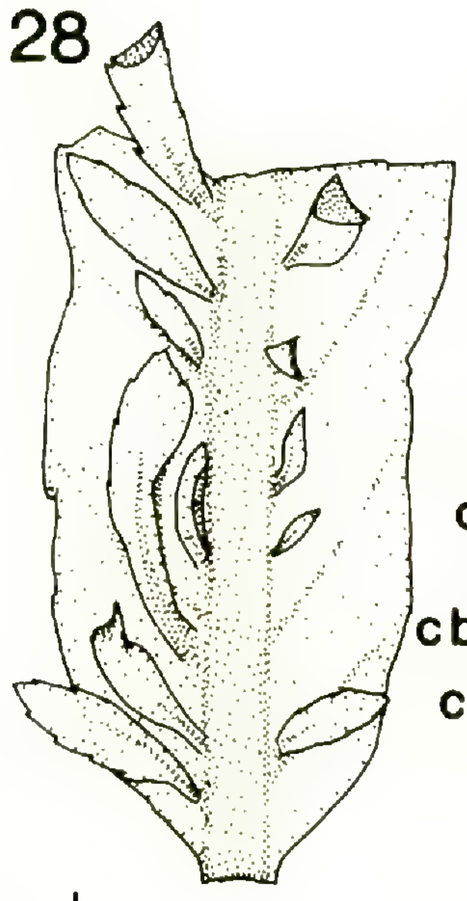


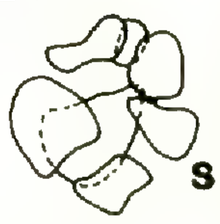


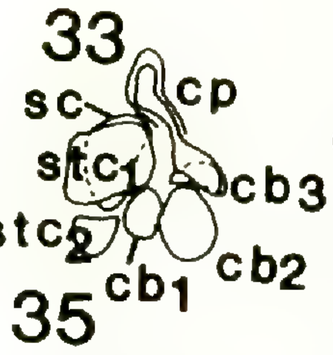


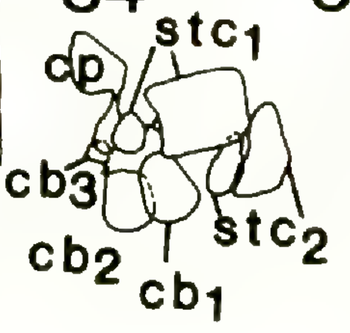


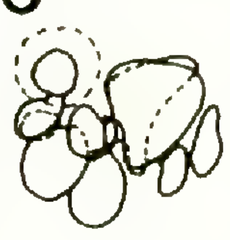


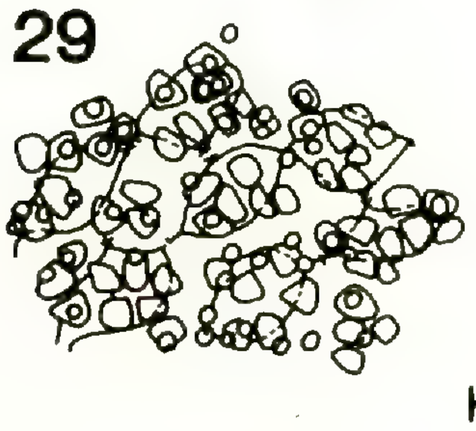












400μm
20

25μm
21–25,29
32–35

3mm
26–28

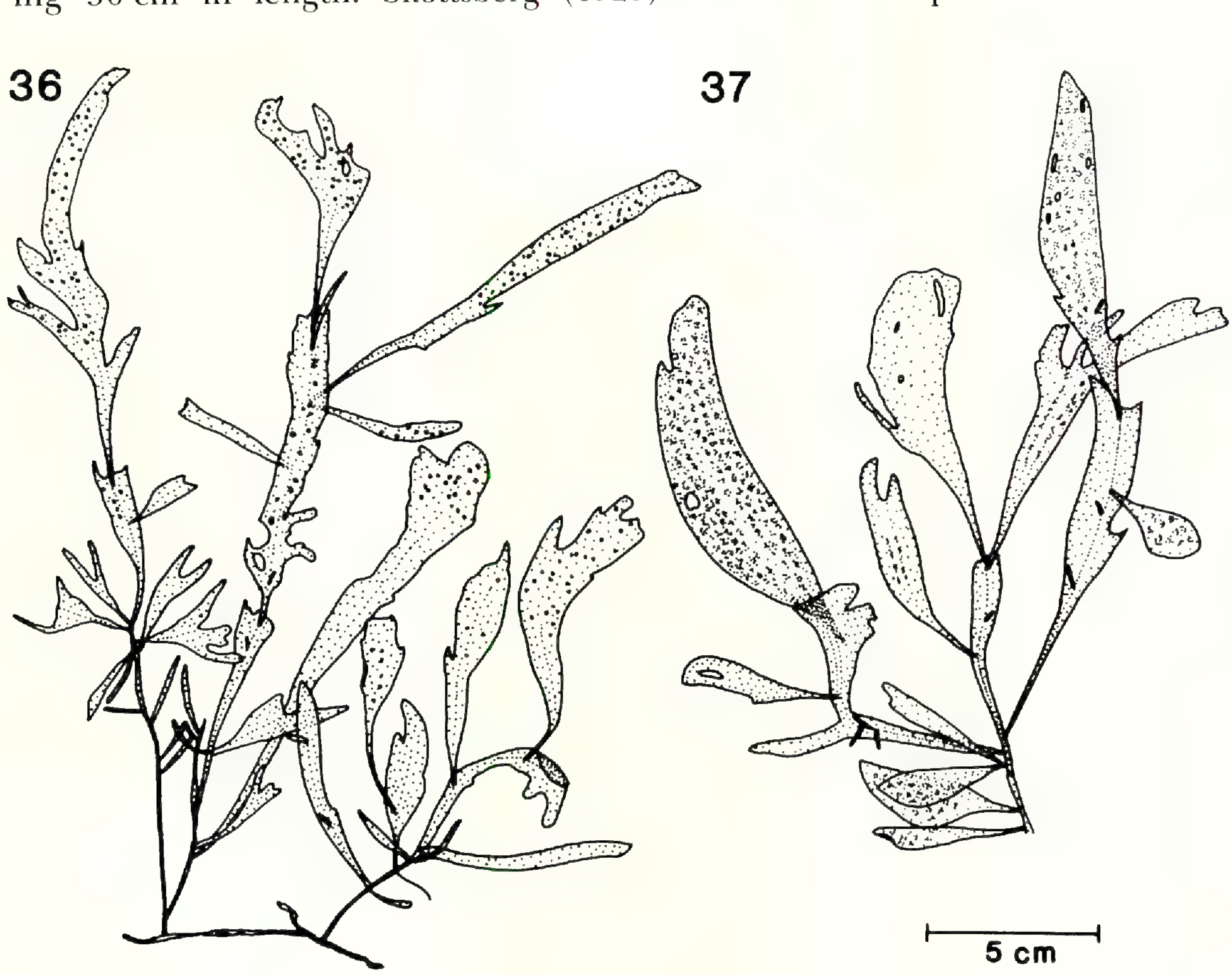
400μm
30,31

FIGS. 20–35. Figs. 20–29 *Phycodrys austro-georgica*; Figs. 30–35 *Neuroglossum ligulatum*. Fig. 20, portion of a blade bearing scattered procarps and young cystocarps; Figs. 21–25, procarps: cb_1,cb_2, cb_3—first, second, and third cells of carpogonial branch, respectively; cp—carpogonium; sc—supporting cell; stc_1, stc_2—first and second group of sterile cells, respectively; Figs. 26 & 27, tetrasporangia-bearing blades; tetrasporangia are produced in midrib-arising leaflets in 26 and in sori on the large blades in 27; Fig. 28, male blades, the spermatangia being produced in leaflets arising from the midrib; Fig. 29, surface view of male bladelet, spermatangia being budded from spermatangial mother cells; Fig. 30, transection of a portion of a blade; Fig. 31, transection of a portion of older midrib; Figs. 32–35, procarps (see above for explanation of symbols).

are absent, as stated by Skottsberg (in Kylin & Skottsberg, 1919). Skottsberg had been able to compare his material with a collection of this species in the Hamburg Museum. The material from Zavodovski I. fully agrees with the photograph of the specimen identified as *N. ligulatum* by Skottsberg and cited in Kylin and Skottsberg (1919).

When Skottsberg (in Kylin & Skottsberg, 1919) transferred Reinsch's *Delesseria ligulata* to this genus, he also asserted that *Choreocolax delesseriae* Reinsch (1890, pl. 15, figs. 4–6) was not a separate organism but in reality represented the early stages in the production of lateral blades from the region of the midrib of *N. ligulatum*. Skottsberg also disagreed with Reinsch's statement that midrib proliferations are lacking in this alga, pointing out that Reinsch's (1890, pl. VI) figure illustrated such proliferations. Zinova (1966) also referred to clusters of small leaves emerging from the midrib of older axes and larger blades. I concur with Skottsberg's and Zinova's characterization of this alga as having lateral blades commonly produced, either singly or in clusters, from the region of the midrib (Figs. 36 & 37). In fact, the occurrence of lateral blades as marginal outgrowths is relatively rare in the specimens at hand. Individual blades become lobed and proliferous along the margins, but the more significant branching system is based on the origin of blades from the midrib rather than from the margins of blades. Reinsch and Skottsberg referred to occasional blades becoming furcate, and I also observed some blades forking. The very different type of branching seen in *N. ligulatum* from that observed in the type species (*N. binderianum*) (cf. Kützing, 1843; Wagner, 1954; Simons, 1976) raises the question whether these two species can be placed in the same genus.

Specimens of *N. ligulatum* from Zavodovski I. are very robust, some reaching 50 cm in length. Skottsberg (1923) referred to a specimen that was



FIGS. 36 & 37. *Neuroglossum ligulatum*. Fig. 36, portion of a cystocarpic specimen; Fig. 37, portion of a tetrasporic specimen.

60 cm in length. Blades can be 10–12 (occasionally to 14) cm long and are usually 1–2 cm wide but occasionally reach 3.5 cm in width. Lateral venation is absent. Skottsberg (1923) remarked that a single apical cell could be detected in the "almost microscopic proliferations" and that the leaflets had assumed marginal growth by the time they were a few mm long. Present observations revealed a single apical cell was present in proliferations (in the tufts arising from the midrib) less than 1 mm in length. But by the time they are 1 mm long marginal growth has become active, and the single apical cell is no longer evident by the time the proliferation is 2 mm long.

Male, female/cystocarpic, and tetrasporangial specimens are represented in the collections from Zavodavski I. Examination of male blades showed that close to the margin primary cells cut off a cortical cell to either blade surface by periclinal divisions. These cortical cells then undergo a series of anticlinal divisions such that each produces about 16 cells (a range of 8 to 20 cells) that function as spermatangial mother cells. One sees in sectioned, reproductively mature blades a tristromatic structure: a central layer of relatively large cells and numerous smaller flask-shaped spermatangial mother cells on either surface. The spermatangial mother cells cut off single spermatangia outwardly.

On female blades the procarps are randomly scattered over the blade surfaces. Each procarp consists of a single four-celled carpogonial branch and two sterile-cell groups, each consisting of one or two cells (Figs. 32–35). This procarp pattern is the *Myriogramme*-type (Kylin, 1924). The scattered cystocarps are 1.5–2.0 mm in diam. Skottsberg (in Kylin & Skottsberg, 1919) referred to the cystocarp of *N. ligulatum* as having a thick papilla or crown perforated by an ostiolar canal, which he indicated as characteristic of the genus.

The cystocarp of this species, when observed in section, seems to be intermediate between the *Schizoseris*-type and the *Gonimocolax*-type (Kylin, 1924), even though that of *N. binderianum* conforms to the *Schizoseris*-type (Kylin, 1924; Wagner, 1954). The carposporangia are ovoid to tear-shaped, reach 90 μm in length, and are arranged in chains. They are produced on elaborately branched gonimoblast filaments that arise from a much dissected fusion cell (of about 225–285 μm diam.). The fusion cell is connected by processes to numerous content-rich central cells on the floor of the cystocarp, which is similar to the *Gonimocolax*-type of cystocarp. But the discrepancy with that type is the presence of a fusion cell in the cystocarp of *N. ligulatm.* The discrepancy with the *Schizoseris*-type cystocarp is the presence of the numerous content-rich primary cells and the connections of processes from the fusion cell with those primary cells as well as the fact that the gonimoblast filaments are not all completely converted into carposporangia, in contrast to the situation in *N. binderianum* (Wagner, 1954). This difference in the organization of the cystocarp may be further evidence that *N. ligulatum* should not be placed in *Neuroglossum.*

Skottsberg (in Kylin & Skottsberg, 1919) described the tetrasporangial sori as being sharply delimited, oval, a few mm in diam., and developing between the midrib and the margin. I observed tetrasporangial sori also to be oval, about 0.8 by 1.2 mm, and first appearing near the margins of the lower half of the blade. In later stages the initially discrete sori often coalesce into irregularly linear extensions running lengthwide on the blade, to 1 cm long or more but only 1 mm broad. These sori generally cover the entire blade but leave a central clear zone, corresponding to the midrib, in the lower half of the blade.

Neuroglossum, based upon *N. binderianum*, is most closely related to *Platyclinia*, another genus of the *Myriogramme* group of Kylin with a Southern Hemisphere distribution. Both genera have polystromatic blades, which show a similar appearance in section: a gradual reduction in size from the largest medullary cells seen as a median row to the smaller medullary cells on either side of the central row finally to the smallest cells of the cortical layers, which is also

true of the anatomy of *N. ligulatum* (Figs. 30 & 31; cf. also Reinsch, 1890, pl. VII, figs. 7 & 8; Skottsberg, 1923, fig. 19c). The two genera were separated by Kylin (1956) on the basis that the midrib is detectable only near the base in *Platyclinia* but continues into more distal portions of the blades in *Neuroglossum*.

SUMMARY

Four species of Delesseriaceae are recorded from the South Sandwich Islands in the Antarctic. *Delessaria salicifolia* is shown to include *D. stephanocarpa* on the basis of the morphological similarity of their vegetative habit and of their special female and tetrasporic leaflets. *Microrhinus carnosus* is transferred to the *Delesseria* group, and its strong resemblance to *Yamadaphycus carnosus* is pointed out. Procarps of *Phycodrys austro-georgica* and *Neuroglossum ligulatum* are figured. The former species conforms to the genus *Phycodrys* despite the unusual branching pattern, whereas the latter species seems less closely related to the genus *Neuroglossum*. The production of clusters of vegetative leaflets from the midrib in *N. ligulatum*, which then develop into the indeterminate branch system, is unlike the branching pattern present in *N. binderianum*, the type of the genus.

ACKNOWLEDGMENTS

I wish to thank Dr. Michael A. Hoban for providing me with these collections made on the research vessel *Islas Orcadas*, while he was a participant on a joint cruise (no. 17–78, Stat. 29) of the National Science Foundation and the Argentine Navy. Dr. Hoban's participation in the cruise was made possible by NSF grants (DPP 76-80738 and DPP 78-23463) to Dr. Greta Fryxell, and her assistance is also gratefully acknowledged. I am also most grateful to Mr. Richard L. Moe and Dr. Max H. Hommersand for their careful reading of the manuscript and offering much useful criticism.

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